University of Manitoba

FOOD HABITS, GASTRIC DIGESTION AND FOOD CONSUMPTION RATES OF YELLOW PERCH, Perca fluviatilis flavescens (MITCHILL), IN WEST BLUE LAKE, MANITOBA

by

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ABSTRACT

Food habits and rates of digestion and food consumption were determined for yellow perch in West Blue Lake, Manitoba during the spring and summer of 1969 and 1970. Perch were diurnal in both swimming and feeding activity. Composition and amount of food eaten by perch varied with time of day, season and size of fish. The greatest feeding activity generally occurred during mid-morning and early evening. Chaoborus sp pupae and cladocerans tended to be eaten in early morning and late evening while benthic organisms and fishes were eaten throughout the day. Seasonally, major components of the diet of adult perch were amphipods and immature aquatic insects in spring and early summer with fishes and crayfish predominating in late summer. For juvenile perch, cladocerans and amphipods were eaten in early and late summer with amphipods and fishes predominating in mid-summer. Weight of stomach contents increased with fish weight but not in a direct proportion. Cladocerans decreased in importance in the diet with increasing fish size while fishes and crayfish increased. Of the two species of amphipods in West Blue Lake, Gammarus lacustris tended to be eaten by adult perch while Hyalella azteca were eaten by juvenile perch.

The times to 95% digestion for amphipods, sticklebacks and crayfish were estimated to be 10.5 (11.5 - 16.0 C), 36 (15 C) and 56 (20 C) hrs, respectively, by adult perch. For

juvenile perch the times were calculated to be 32 (15 C), 38 (20 C) and 72 (13 C) hr respectively. Digestion rates were related to size and structure of the food items and water temperature.

A method was devised to estimate average daily food consumption for juvenile perch from knowledge of their diurnal feeding patterns and gastric digestion rates. Estimates were 2.7, 3.5, 3.1 to 3.6% of body weight (wet weight) for June, July, August and September of 1970 respectively. Changes in these values corresponded with the mean monthly degree of stomach fulness and were independent of daylength and temperature. Comparisons of calculated calorific intake to estimated metabolic expenditures verified that there was sufficient energy available for growth and reproduction.

Amphipods formed the basic food item for perch in West Blue Lake. Cladocerans, immature dipterans, crayfish and fishes were of secondary importance while insects other than dipterans were of minor importance. Perch were classified as both secondary and tertiary consumers deriving approximately equal portions of their diet by weight from benthic and pelagic organisms (primary consumers) as well as from fishes (secondary consumers).

INTRODUCTION

Many studies, frequently with different purposes, have been carried out on the kinds and amount of food eaten by yellow perch. Some describe the food organisms present in stomachs collected at a particular time (Nurnberger, 1930; Ewers, 1934), but often food habits related to size (Allen, 1935), season (Langford and Martin, 1940) or time of day (Keast and Welsh, 1968) have been investigated. Others describe, feeding relative to food availability (Keast, 1965) and food selection (Galbraith, 1967) or interspecific competition (Dunn, 1954).

The purpose of the present study is to describe and quantify the food and feeding habits of yellow perch in West Blue Lake, where the ultimate research objective is to describe in quantitative terms, energy exchanges and pathways in this aquatic ecosystem. Initial stages of this project require knowledge of plant and animal communities within the system and their relative importance in the flow of energy through the various pathways.

In this study, I examined the food organisms in the diet of juvenile and adult perch during the spring and summer of 1969 and 1970 relative to time of day, season and fish size. In addition, I studied gastric digestion rates of natural food organisms and estimated average daily food consumption.

LITERATURE REVIEW

Pandian (1967) described food consumption, digestion, absorption and conversion as successive steps involved in the transformation of food into animal tissue. Gerking (1962) emphasized the importance of knowledge concerning the food habits of fishes in determining fish production and food utilization. In this review, only literature pertaining to the underlying principles, methods of study and factors influencing food and feeding habits, food consumption and digestion by fishes are presented with reference to yellow perch when possible. First a brief review of the biology of yellow perch is given.

Biology of the Yellow Perch

The yellow perch, Perca fluviatilis flavescens (Mitchill) Percidae, has a terminal mouth, two separate dorsal fins, a compressed green and yellow fusiform body with six to eight dark, vertical bars (McPhail and Lindsey, 1970). It is distributed throughout temperate North America where its range extends from the Lesser Slave Lake and Hudson Bay drainages, east to New Brunswick, south to South Carolina and west to Kansas. It has also been successfully introduced into many other areas. In northern Asia and Europe the yellow perch is classified as P. f. fluviatilis and is morphologically similar to the North American form. The yellow perch is essentially a lake fish, but may also inhabit slow moving rivers,

creeks and ditches. They are most numerous in open and moderate to highly fertile lakes.

Life History - Perch spawn in spring, the exact time depending largely on water temperature. Shoreward migration occurs after ice break-up, usually in April or May, at water temperatures from 2.2 to 6.8 C (Muncy, 1962). Spawning takes place at temperatures from 7 to 10 C in depths of 1 to 3 m on sand, gravel or vegetation where the eggs are laid in long gelatinous ribbons (Herman et al, 1959). Males often out number the females on the spawning grounds and are first to arrive and last to leave (Alm, 1954). On the average, females deposit 23,000 eggs with the number depending on size and condition of the fish (Sheri and Power, 1969).

The development time is usually from 8 to 10 days but depends on water temperature (Herman et al, 1959). The time between initial spawning and hatching was approximately 24 days (Echo, 1954). Houde (1969) has shown that fry are pelagic from the time of hatching while Maloney and Johnson (1957) showed that fry remained in the shallows periodically before becoming pelagic. In this period, fry tend to be evenly distributed throughout the surface layers of the lake (Faber, 1967). In mid-summer they move to the littoral regions and remain closely associated with the shore until later years when they inhabit deeper regions of a lake (Eschmeyer, 1938).

Alm (1946), on the basis of work done by Walter (1934)

and Roper (1936) distinguished three coexisting forms of perch. One frequenting vegetation close to shore and feeding on littoral organisms had a compressed body shape and vivid coloration. Another, a piscivorous form, lived in deep water, was more fusiform and had a dull coloration. The third form, living near the surface, was also dull in color but ate both fish and plankton. These three forms had different growth rates.

Migration - Yellow perch exhibit well marked seasonal and daily migrations which may vary between lakes or between locations within a lake. During ice-cover perch inhabit the mid-water regions, moving slowly in loosely associated schools (Hergenrader and Hasler, 1966). In early spring there is an inshore spawning migration which corresponds to an increase of water temperature and maturation of the gonads in adult perch (Allen, 1935). Soon after spawning, perch move into deeper water until the formation of a thermocline (Maloney, 1969). Throughout the summer perch tend to remain in the region above the thermocline with an average thermal distribution of 21 C (Ferguson, 1958). Horak and Tanner (1964) found that the depth distribution of perch increased over the summer but was not correlated with temperature. Their swimming speed increases with water temperature up to 20-25 C, and then decreases (Hergenrader and Hasler, 1967-a). They aggregate in tighter schools (Hergenrader and Hasler, 1967-b) at higher temperatures.

Perch undertake daily migrations which are probably related to feeding behaviour (Evermann and Clark, 1920), but whether these migrations are a direct or indirect response is not clear. Hasler and Bardach (1949) observed that perch in Lake Mendota migrated inshore and then parellel to shore at the six m contour from 40 to 60 min before sunset. A less clear-cut migration was observed after sunrise. Hasler and Villemonte (1953) noted that schools of perch broke up at sunset and settled to the bottom where they remained motionless. At sunrise they rose from the bottom and moved into deeper water. Scott (1955) has shown that migration patterns of perch are complicated by the presence of migratory and non-migratory young perch as well as older migratory perch, each exhibiting differences in behaviour. The diurnal activity of perch is generally bimodal with either the greatest activity at sunrise (Sieh and Parsons, 1950) or sunset (Brown and Rosen, 1957). However, Carlander and Cleary (1949) showed perch to be most active in the afternoon and early evening. In general, there is a sunrise peak in activity which tapers off and an abrupt evening peak. However, numbers caught reflect both activity and local perch abundance (Scott, 1955). Spencer (1939), by laboratory experiments, showed that perch were active only during the day and exhibit sporadic activity. Bardach (1955) has shown that the depth at which they are located during the day and the extent of the migration both depend on the depth of the

thermocline. Alabaster and Robertson (1961) demonstrated that a combination of dissolved oxygen, temperature and light influence their diurnal activity. Under the ice, perch undergo diel vertical movements with a mid-afternoon peak in activity (Hergenrader and Hasler, 1966).

Food and Feeding Habits - Pearse and Achtengerg (1920) described the yellow perch as a versatile feeder. Feeding usually takes place on or near the bottom but has also been reported to feed in mid-water (Keast and Webb, 1966), and on occasion at the surface (Coots, 1956). With their sharp, backward-directed teeth, perch are efficient predators, but their slender gill rakers also enable them to filter small organisms such as zooplankton. Turner (1920) described young perch as generalized feeders since they are limited to small food organisms.

Variations in available food organisms in different parts of its range make compilation of a dietary list difficult. However, certain generalizations may be made. Size of perch is a major factor in determining feeding habits in a given habitat. Nurnberger (1930) reported that the food of perch from 17-50 mm was largely zooplankton; while those from 50-100 mm fed on insects, and those from 100-390 mm fed on fish and crayfish. Allen (1935) found a gradual transition in diet as perch became older. Perch less than 165 mm fed on zooplankton, those from 115-190 mm fed on bottom organisms and those greater than 165 mm fed on fish. Turner (1920), Tharratt (1959) and Antosiak (1963) had similar results with

local variations. Diet of young-of-the-year perch is predominately zooplankton (Pycha and Smith, 1954; Maloney and Johnson, 1957). Greatest variation occurs in adult perch where the various dominant food organisms were crayfish (Eschmeyer, 1937; Harlan and Speaker, 1951), Entomostraca (Pearse and Achtenburg, 1920), fish (McCormack, 1970). Cannibalism is also very common in larger fish (Coots, 1956). Allen (1935) found that larger fish had a greater percentage of empty stomachs.

Seasonal changes in food habits of perch were largely influenced by changes in food abundance and the regions inhabited (Pearse and Achtenburg, 1920). Greatest stomach volumes were found in early spring, and smallest in winter (Seaburg and Moyle, 1964). Fisk (1953) reported insects to be dominant in winter and spring, with fish dominant in summer and autumn. In constrast, McCormack (1970) found amphipods to be the dominant food in spring, plankton and fish in summer, and plankton in fall. Feeding of perch in winter is less diversified and cannibalism increases (Antosiac, 1963). Moffet and Hunt (1945) found that the volume of stomach contents were small in winter with zooplankton, immature insects and fish being the major items in the diet. In addition, the frequency of empty stomachs was higher in the winter (Allen, 1935). Pearse (1918) reported that perch were active winter feeders, but feeding was suspended to spawning.

Keast and Welsh (1968) showed that perch had a diurnal feeding pattern with two peaks, each coinciding with activity.

Stomach weight was greatest during the evening peak and the same food organisms were ingested all day. Keast and Welsh (1968) and Muncy (1962) found that the frequency of empty stomachs was greatest at night.

Sexual differences in feeding behaviour between sexes of mature perch have been observed by Tharratt (1959) and Eschmeyer (1938) due to differences in distribution caused by temperature preferences. Males fed on the bottom and females in open water.

Local variations of substrate and vegetation may influence the food habits of perch. Turner (1920) found differences in stomach contents between stations, whereas Ewers (1934) found little variation. Pearse and Achtenburg (1920) described differences in food habits related to depth and diurnal variations in catches which indicated feeding in deep water prior to an onshore feeding migration.

Feeding Habits of Fishes

Feeding is a basic function of an organism since through ingested food, energy is provided to respire, grow and reproduce (Nikolsky, 1963). One studies food habits of fish species to understand the qualitative and quantitative connection between fish and their food organisms. The type of feeding varies among species making generalizations difficult. However, fish can generally be grouped into herbivorous, detritophagus and carnivorous feeders with each species adapted to feed on a particular food or a variety of foods by its

morphology, sensory organs, buccal cacity and alimentary canal (Nikolsky, 1963).

Definition of Terms - A number of terms are used in this review which need clarification since the meanings are often not self-explanatory. Food habits usually refer to the food eaten, as estimated from the relative composition of food items in the stomach, while feeding habits refer to the manner in which food is captured, consumed and how food habits vary with respect to time of day, season or size and species of the consumer. Predation, in its purest sense, means the capture and consumption for food of one animal by another (Salt, 1967). The frequency of individuals in the diet of a predator is determined by characteristics of the prey species such as abundance (frequency in the environment), availability (exposed or hidden due to cover) and distribution (clumped or dispersed). Also the diet may be influenced by characteristics of the predator such as selectivity where unfit, conspicuous or a certain size of prey is eaten or innate preference where prey species may be chosen or rejected due to physical or chemical characteristics.

Ingestion may be defined as the total uptake by a population of heterotrophic organisms, while consumption is ingestion during a specified time interval (Davis and Warren, 1968). The satiation amount is the quantity of food ingested until an organism cannot take anymore (Ishiwata, 1968-a). The daily meal is the amount of food consumed per day while the daily ration is the daily meal expressed as a percentage of body weight (Ricker, 1946). Finally, digestion is referred

to as the process by which food is broken down into units which may be absorbed through the gut wall and the rate of digestion is defined as the number of hours required to pass all food from the stomach to the intestine (Windell, 1968).

Factors Affecting Feeding - Feeding habits vary greatly among species and among individuals and populations of the same species, but there are factors which limit or influence feeding. In addition to abundance, availability, distribution, behaviour and size of the food organisms and size, sex and behaviour of the consumer, competition from other fish species and abiotic conditions are important in affecting feeding.

Gerking (1962) suggested that each population has its own habits which are related to food preference and the relative abundance of different food organisms. Hess and Swartz (1941) stated that "the kind and amount of food eaten is a result of interaction of the fish, the food organisms and the environment." The composition of food in the stomachs of fish is not necessarily indicative of the abundance of food organisms present in the environment. Borutsky (1960) distinguished between the forage resource, "total complex of animal and vegetable organisms and their decomposition products," and the forage base, "that part of the forage resource utilized by the existent fish population." Prey species may either be unavailable to the predator due to cover or be rejected due to characteristics such as spines or taste. Ivlev (1961) found different fish species to "prefer" certain food species and select prey within definite

size limits or those which moved at particular speeds. Allen (1941) distinguished between apparent selection (a result of different levels of feeding activity) and real selection (a result of active choice by the consumer). Apparent selection of food items was low during the initial stages of feeding but increased when stomachs became full. Galbraith (1967) and Cooper (1965) reported that yellow perch tend to select prey within certain limits of size.

Seasonal variations in food eaten are primarily caused by differences in the composition, abundance and availability of food organisms and are modified by the fishe's adaption to abiotic conditions (Nikolsky, 1963). In summer, the variety and quantity of food items occurring in fish stomachs is greater than in winter (Keast, 1968). The daily feeding pattern is largely influenced by light through the orientation of the predator to its prey and behaviour of the food organisms. Hoar (1942) showed that the daily feeding pattern for trout (Salvelinus fontinalis) and young salmon (Salmo salar) is modified by light and temperature. Northcote et al (1964) found that adult kokanee, Oncorhynchus nerka, and peamouth chub, Mylocheilus caurinum, underwent diel vertical movements in response to light. The movements were probably feeding and protective in nature. The periodicity and nature of the food organisms vary with different consumer species: eg., diurnal, nocturnal and continuous feeders (Keast and Welsh, 1968).

Elton (1927) stated that "any one species of animal eats

food only between certain limits of size and that size of food is one of the main reasons underlying the existence of food chains." The increase of food size with an increase of fish size has been demonstrated in most fish (Allen, 1935; Lindstrom, 1955) but is subject to strong variation. Hartman (1958) showed that, in general, the size of food eaten was proportional to the mouth size of the consumer, but some food items were rejected at larger sizes because of characteristics of the prey. Generally, the number of food organisms found in the stomach decreases as the fish grows while the size of individual food organisms increases (Nikolsky, 1963). The reason for this trend is that, as a fish grows, more individuals of a particular food organism are required and the energy expended in search and capture of the food organisms may become greater than the energy content. Consequently, the fish has to change to larger food organisms with higher energy value per unit and requiring less energy expenditure per unit for capture (Allen, 1935). In conjunction, the mouth size increases proportionately with fish size to cope with larger food organisms.

Feeding habits are also modified by the concentration of the predator and type of feeding. For example, plankton feeders feed heavily in aggregations while predatory fish feed more when solitary (Nikolsky, 1963). Hartley (1948) demonstrated that, within a community of fish, there were various modes of feeding with differences in pattern. He reported, as did Mann and Orr (1969) and Ball (1948), that

no two species had similar diets but competition did exist for certain staple foods, depending on their relative abundance.

Methods of Study - Fish have been collected for stomach analysis by a variety of gear, such as trap nets, gill nets and seines. Also, poisons and electrical shocking have been used. Use of a collecting method depends on the situation and gear characteristics. After collection, fish are killed and preserved to prevent decomposition of the stomach contents (Ball, 1948). The usual method of preservation is to kill the fish to prevent regurgitation (Turner, 1955), and slit the body wall to facilitate rapid penetration of the preservative (5-10% formalin or 70% ethyl alcohol).

Many methods have been used in stomach content analysis. The choice of which depends largely on the type of study undertaken. Some authors have analysed intestinal contents as well but this review will be limited to stomach analysis. Most studies involve analysis of individuals but fish may be grouped according to location and size (Borgeson, 1963). This method, although more rapid, gives no indication of individual variation. Analysis of individual stomachs usually involves determining the frequency of stomachs in which food items occur, their average or relative percentage by number, weight and/or volume. Volumes have either been determined by volume displacement or estimated by comparison to objects of known volume (Larimore, 1957). Weights have been measured as blotted wet weights, dry weights or dried digestible organic

material (Windell, 1968).

Usually occurrence, numbers and weight or volume are determined for the food habits of a particular fish species. The occurrence method demonstrates what organisms are being fed upon but gives no information on quantities or numbers and does not take into consideration the accumulation of food items resistant to digestion. Likewise the numerical method gives no indication of relative bulk and does not account for food items which accumulate in the stomach. Volumetric and weight studies alone tend to mask the importance of the smaller food items. Data may be much distorted by the occasional occurrence of an exceptionally bulky food item, which may be digested quite slowly (Windell, 1968). Tester (1932) plotted volume against frequency of occurrence and obtained rectangles with arbitrary ratios. The geometric mean of the volume and numerical indices or the sum of their logarithms may also be expressed. A points system for ranking items in the stomach was first proposed by Swynnerton and Worthington (1940) and later modified and recommended by Hynes (1950). In this method rank numbers are assigned to food organisms in the stomach; the number assigned depending on the size or abundance. All assigned numbers for each food organism are summed and scaled down to percentages. Disadvantages to this method are that results are arbitrary and data cannot be used for comparisons. In another rank method, Beck (1952) suggested that a food index could be obtained by multiplying the percent frequency of occurrence,

percent by volume and the specific gravity of the food items.

Often the relative abundance of bottom and planktonic organisms in the environment are sampled along with stomach sampling. From this the degree of selectivity exercised by fish can be determined (Surber, 1930). Hess and Swartz (1941) used the "forage ratio" (ratio of the percentage composition of a food item in the diet to the percentage of the same food item in the environment). A ratio greater than unity indicates selection while a ratio less than unity indicates selection against.

In some studies, reconstruction of various food organisms has been carried out in order to determine food values (Skalkin, 1965). Size or number of undigested food organisms is extrapolated from partially digested remains. Reconstruction is usually carried out on preserved specimens which shrink and lose weight resulting from the effects of the preservation (Parker, 1963).

One difficulty in interpreting data from stomach analysis is that the variation in the number of food organisms is often greater among the individual fish in a sample than between mean values from different samples. This is apparently because the number of different food organisms in a single stomach is limited, resulting in a Poisson distribution in which means and variances approach equality. (Snedecor and Cochran, 1968). To attain equality of

variances Mann and Orr (1969) analysed square roots of their basic data (Bartlett, 1947). But, because of internal variability, little improvement was achieved. Samples of fish for stomach analysis are assumed to be taken at random from a population of fish. In general, there is great variability in the relative volumes of different food items eaten when the sample size is small. The variability decreases with an increase in sample size until a certain level is reached. Hanson and Graybill (1956) used formulae to determine the number of animals necessary in food habit studies.

In summary, it can be seen that the food and feeding habits of fishes are subject to strong variation making interpretation and analysis difficult. Complete knowledge of the qualitative and quantitative interrelationships between food and consuming organisms are therefore necessary before more sophisticated studies of food consumption, digestion, utilization and growth by a population of fish can be carried out.

Consumption of Food by Fish

By definition consumption is the amount of food ingested over a given interval of time. It is the first step involved in the transfer of food into fish tissue and is of utmost importance in determining conversion efficiencies as described by Lindeman, (1942) and Richman (1958).

Methods - Many methods have been used to determine the food consumption in fishes. These involve either direct or

indirect procedures under laboratory or field conditions. Food consumption is typically measured in the laboratory by the difference between the amount of food presented and the amount of food remaining at the end of a given time period (Hathaway, 1927; Baldwin, 1956; Hunt, 1960). Bajkov (1935) using a direct method estimated the amount of food consumed by whitefish (Coregonus clupeaformis), primarily a night feeder, by doubling the weight of stomach contents of fish caught overnight in gill nets. He also proposed a formula based on the assumption that if the fish in question feeds continuously and all the food passes into the intestine during 24 hours the daily consumption would be a function of the average amount of food and the time necessary to empty the stomach. This method required analysis of stomach contents from one sample and the determination of digestion rate from another. This method is not usually employed because assumptions can seldom be met. Furthermore, effects of handling and of differences in the amount and kind of food were not considered.

Fortunatova (1950) developed an equation to express daily food consumption by predaceous fish, assuming that fish ingest a large prey only once a day. From the food present and reconstruction procedures it was believed possible to determine the date it was consumed and daily ration. Darnell and Meierotto (1962) used the state of digestion of a standard food item as an index to how long food items had been present in the stomach. The total amount of food eaten during any

one time interval or through the day was found by determining the percentage of the standard food item in each stage of digestion and its percentage of the total contents. The percentage of this food item in the stomach for a particular period of time was assumed to be equal to the total contents that had been present during that period. This method assumes that the conditions of the standard food item are truly representative of the conditions of others and the results of laboratory experiments are applicable in the field.

Seaburg and Moyle (1964) calculated the daily consumption of bluegills, Lepomis macrochirus, from the product of the average stomach volume for the summer, the percentage of food found experimentally digested in four hours, and the number of such periods in a day.

Keast and Welsh (1968) determined the mean minimum daily ration of young perch to be two per cent of body weight by adding together the average weight of stomach contents for fish caught during peak feeding periods. This method estimates a minimum value since some food is digested between peak feeding periods.

Hamilton (unpub.) determined the amount of food consumed per day for rainbow trout, Salmo Gairdnerii (Richardson), by measuring the rate of flow of a major food organism through the digestive tract. This was done by first determining the ratio of the number of organisms in the intestine to that of the stomach, thus giving an indication of the relative rate at which food organisms were fragmented to the

point that they could not be counted. The amount of food consumed per day was then calculated by multiplying the number of organisms in the stomach by the above ratio and the daily replacement rate of the food organisms in the gut. Assumptions were that fish exhibited a diurnal feeding behaviour, all food organisms could be counted and identified and all food items pass through the gut at the same rate.

Pinskii (1967) determined the amount of food consumed per day by knowing the difference between maximum and minimum daily indicies of fulness and dividing this difference by the period during which the stomach fulness decreased. The daily ration was obtained by multiplying by 24 and dividing the product by 100. This method does not take into consideration food ingested during the decrease of stomach fulness or digested during an increase.

Indirect methods of estimating food consumption are usually conducted wholly or in part in laboratory aquaria. Difficulties arise in comparing these results to the field since the nature of food is often different and the fishes are subject to stress and decreased activity. Winberg (1956) and Ivlev (1961) have proposed similar equations using growth, temperature and respiration data to determine the daily ration. Winberg (1956) based his method on the assumption that the energy content of the food equals the sum of the energy contents of the material lost in egestion and excretion, and the material retained in growth (somatal and gonadal) and the material broken down in metabolism. He assumed that the physiologically useful food energy was

approximately 80% of the food and excretion with 15 and 3% lost in egestion and excretion respectively. Winberg (1956) used the parabolic relationship between metabolism and body weight and corrections for temperature from the Krogh's normal curve (Ege and Krogh, 1914) to determine resting metabolism and estimate active metabolism in nature. Paloheimo and Dickie (1965, 1966a, 1966b) have reviewed the methods and values used by Winberg (1956) and were in general agreement with his findings.

Surber (1935), Pentelow (1939), Brown (1946) and Johnson (1966) determined food consumption for fish held in captivity. In each case the amount of food required to keep the body weight constant (maintenance ration) and the efficiency in food utilization for growth (ratio between food consumed above the maintenance ratios and the corresponding gain in weight) were determined.

Meine et al (1937) found food consumption in fish held briefly after capture to be a function of the rate of nitrogen loss in feces and through the gills and kidneys. The nitrogen content of previously consumed food was taken to be the sum of the above losses.

Gerking (1962) used a relationship between food consumption and growth rates of bluegills in the laboratory to estimate rates of consumption in the field from growth rates of wild fish. He based calculations on the amount of protein that would have been ingested by the fish to meet growth requirements.

Kevern (1966) used a radioisotope method to estimate the daily consumption for yearling carp (Cyprinus carpio) in the field. The amount of ^{137}Cs that must be ingested as an integral part of the food items to maintain the equilibrium body burden of the carp was calculated from measured values for body burden, biological elimination rates and assimilation factors.

Seaburg and Moyle (1964), Pandian (1970) and Moore (1941) found strong day-to-day variations in daily consumption among individuals since heavy feeding was followed by reduced feeding and required averaging values for several days.

Factors Affecting Consumption - There are a number of environmental variables which influence behaviour and metabolic state, hence food consumption. Among these are temperature, light and dissolved oxygen. Also, the species, sex, size, and condition of the fish influence food consumption. Further, in nature, the concentration and prey preference of fish (Willer, 1929; Kinne, 1960; Ivlev, 1961) plus the abundance, special distribution, availability of food organisms (Allee, 1933; Ivlev, 1961) govern food consumption.

Paloheimo and Dickie (1966a) stated that "at a low level of temperature and feeding an increase of temperature alone may be expected to give rise to a higher metabolic rate, part of which may be expected to result in higher voluntary activity ordinarily resulting in long term higher food uptake." Baldwin (1956) found that the weekly food consumption of brook trout (Salvelinus fontinalis) doubled for each 4C rise

until 13C but decreased with further temperature increase. The food intake of yearling sockeye salmon (Oncorhynchus nerka) increased with temperature to 15-17C then decreased (Brett and Higgs, 1970). Marcus (1932) observed that small largemouth bass Huro floridana, consumed small amounts of food while larger individuals ceased to feed below 10 C.

A direct relation was found between food consumption and average daylength for the green sunfish, Lepomis cyanellus (Refinesque), by Gross et al (1965) while Anderson (1959) showed no such relation for bluegills. Herrmann et al (1962) for coho salmon, Oncorhynchus kisutch, and Stewart et al (1967) for largemouth bass, showed that food consumption decreased with a decrease of dissolved oxygen.

A proportionate in food consumption with increasing body size has been reported for laboratory and field situations by many authors (Hathaway, 1927; Marcus, 1932; Pinskii, 1967; Pandian, 1970). There may, however, be a compensatory effect. Protein content of the food tends to increase with size of the fish (Seaburg and Moyle, 1964; Pinskii, 1967). Pandian (1970) found that females of Limanda limanda tended to consume more than males and there were no differences in food consumption when the nutritive values of rations were different. Swift (1955) demonstrated that food consumption for Salmo trutta varied seasonally, depending upon the condition of the fish and metabolic state influenced by thyroid activity.

Consumption of food varies among fish species according

to their feeding habits. Moore (1941) showed that yellow perch prefer to ingest a quota of food at a single feeding period rather than two at a ratio of 2.6 to 1. Although perch accepted food more frequently than once a day, the total amount, when averaged over a week, was not significantly different than that calculated from a single feeding. The skipjack tuna (Katsuwonus pelamis), fed at intervals by Magnuson (1969), consumed more at certain intervals during the day than at others although feeding was continuous. Feeding rate was highest after periods of starvation, but response to food decreased as the stomach filled. It increased again after the stomach began to empty.

Anderson (1959) with bluegill and Brown (1946) with brown trout (Salmo trutta) found reduced rates of food consumption during the late summer, fall and winter even though the fish were held at constant temperatures. These workers suggested that this phenomenon may be hormonally controlled.

Ishiwata (1968-a) determined the satiation amount for a variety of fish species. He found that this amount varied with acclimatization, hunger, type of food and species of fish (Ishiwata, 1968-b). The satiation amount increased proportionately to body weight but the satiation ratio (satiation amount/body weight) declined with body weight since smaller fish have proportionately larger stomachs. Ishiwata (1969) also showed that as the frequency of feeding increased the daily ration increased but a maximum value was soon reached. The satiation amount was greatest with one feeding

a day and decreased with increased frequency of feeding.

At levels below maximum ration there is some evidence that feeding is proportional to availability of the food organisms (Ricker, 1941). Ivlev (1945) found that with increasing availability of food, the daily ration approached a maximum ration according to an exponential formula.

Digestion Rates in Fish

The process of digestion varies among species of fish largely depending on the type of food, digestive enzymes and morphology of the alimentary canal (Barrington, 1957). Generally, food is ingested whole where it is acted on by stomach acids and enzymes. When digestion is sufficient or when more food is ingested, food is passed to the intestine. Smit (1967) found that gastric reaction of fish may be evoked by a tactile stimulus. He showed that the composition of the gastric juice is determined by the secretory rate which in turn is temperature dependent. At increasing rates of secretion the acid and pepsin outputs and acidity increased but, the pepsin concentration remained constant.

Methods - Digestion rate in fishes may be determined directly or indirectly. Using the direct method, fish are fed a known ration of food and its rate of disappearance from the stomach is determined (Windell, 1968). Variations in this method result from variations in experimental facilities, methods of feeding and type of analysis. Usually experiments are conducted in a laboratory over a range of

temperatures with either natural or prepared food items. The result of these experiments cannot be taken as absolute measures since activity (Tyler, 1970) and handling have some effect on the rate of digestion.

Feeding may take place by voluntary consumption, with conditioned fish (Kitchell and Windell, 1968) or induced by force feeding (Hunt, 1960) using forceps or an injection device (Dill, 1969). Force fed fish may be adversely affected or may subsequently regurgitate food but no positive evidence of these limitations to the method have been presented (Hess and Rainwater, 1939; Hunt, 1960). Stomach contents may be removed at intervals after feeding by either dissection, pumping (Seaburg, 1957) or emetics (Jernejcic, 1969). Stomach contents may then be measured either by blotted wet weight, dry weight, volume (Hunt, 1960) or dried digestible organic matter (Windell, 1966; 1968). Results may be either compared to the original food value and expressed as a percentage or in terms of body weight and a digestion rate curve plotted. In addition, the rate of digestion may be determined by defining arbitrary stages in the digestion process (Armstrong and Blackett, 1969) or by noting the progression of indicator food items through the gut (Webster, 1942 ; Darnell and Meieretto, 1962).

Molnár and Tölg (1962-a, 1962-b) utilized radiography as an indirect method to determine the rate of digestion for predatory fishes. In this method fish were fed an aliquot of food and, by repeated X-rays, the time taken for

food to disappear from the stomach may be determined. The method depends on skeletal structures of the food organisms and requires distortion of the swimbladder to determine the presence of food in the stomach.

Factors Affecting Digestion Rate - Digestion rates vary between species of fish (Seaburg and Moyle, 1964; Kaiya, 1969) and between equal sized individuals of the same species (Hunt, 1960). Hunt (1960) and Pandian (1967) reported that they decreased with increasing age.

Metabolism of fishes (poikilotherms) is regulated by environmental temperatures. Digestion rate is determined by enzymatic action, gastric juice secretion and stomach motility which are in turn, influenced by temperature. Smit (1967), Molnár et al (1967) and, Brett and Higgs (1970) showed that digestion rate increased with increasing temperatures reaching a maximum rate as the upper limit of temperature tolerance was approached. However, Tyler (1970) found young cod, Gadus morhus, to have an optimum digestion rate at 15 C. Molnár and Tölg (1962-b) demonstrated that the relation between digestion rate and temperature for pike perch, Lucioperca lucioperca, was linear when plotted on double logarithmic axis.

Digestion rate also depends on the type, amount and chemical composition of individual food items as well as the species composition of the food. Windell (1967) found bluegill sunfish to have approximately similar digestion times for food organisms of different chemical composition;

consequently a mixed meal had a digestion rate equal to the average of individual food items. Nikolsky (1963) and Hess and Rainwater (1939) reported that soft bodied insects had faster rates than hard bodied ones. In hard bodied forms, sclerites remained in the stomach longer and were eventually aided in passage through the stomach by continuous feeding. Hunt (1960) and Tyler (1970) showed that the rate of passage into the intestine increased with meal size, although Dawes (1931) and Barrington (1957) found that, individually, smaller food organisms were digested quicker than larger items. Further, Dill (1970) showed that as the number of sockeye salmon fry, Oncorhynchus nerka, fed to the whitefish, Prosopium williamsoni, was increased, the time to complete digestion also increased. Protein is digested at a faster rate than fat (Windell et al, 1969). Finally, Dawes (1931) reported that the rate of passage of food through the stomach is related to the amount of food recently consumed (ie. partly digested organisms pass into the intestine when the stomach becomes full). However, bluegills, when fed to capacity rejected additional food and did not resume feeding until some food had passed into the intestine (Windell, 1967).

Windell et al. (1969) proposed three stages in digestion; 1) a lag phase where initial breakdown of the food organism(s) occurs; 2) a surge of gastric activity where the bulk of the food is removed from the stomach; 3) a period when gastric activity and stomach motility is not efficient in removing the remaining food. A direct semilogarthmic rela-

tionship between stomach fulness and time was demonstrated by Tyler (1970). He proposed that this relationship could be explained by the surface area or volume of the food and that digestion rate was mainly dependent on the quantity of food present in the stomach. Exception to these curvilinear relationships occur and the resulting data often approach straight lines (Windell, 1966; Kitchell and Windell, 1968). Pandian (1967) found that, after an initial lag, the percentage of food digested by Megalops cyprinoides and Ophiocephalus striatus varied directly with time. Magnuson (1969) used polynomial regression to account for a slight curvilinear feature.

MATERIALS AND METHODS

Description of the Area

West Blue Lake (Fig. 1) is a "channel lake", located in the Duck Mountain Provincial Park, in western Manitoba (lat. 50^{o} 31'; long. 100^{o} 55') (Bell and Ward, 1971). It has three distinct basins which have a total surface area of 160 ha and a volume of approximately 92 x 10^{6} m^{3}. Mean and maximum depths are 11.3 and 31m respectively. The lake is essentially a closed system with steep sides and limited littoral regions. It is a dimictic lake (Hutchinson, 1957), with ice cover from November to May. The average day length varies from 7 to 8 hours in winter and 15 to 16 hours in the summer (Fig. 2-A). Between 1969-1970 surface temperatures varied from 0 C to 19-20 C while the average temperatures (upper 20m) varied from 3 C to 11-13 C respectively (Fig. 2-B). The lake stratifies thermally during summer (Fig. 3), often causing severe oxygen depletion below 20m.

There are a variety of organisms in West Blue Lake. Zooplankton consists of Rotifera (Keratella cochlearis, K. quadrata, Felinia longiseta and Asplanchna sp.). Copepoda (Diaptomus siciloides and Cyclops bicuspidatus), Cladocera (predominately Daphnia pulex; rarely Bosmina sp., Epischera lacustris and Megalops edax) and Chaoborus sp. (Biette, unpub.). Benthos is primarily composed of Amphipoda (Gammarus lacustris lacustris and Hyalella azteca), Decapoda, Orconectes virilis,

Fig. 1 Bathymetric map of West Blue Lake showing sampling locations.

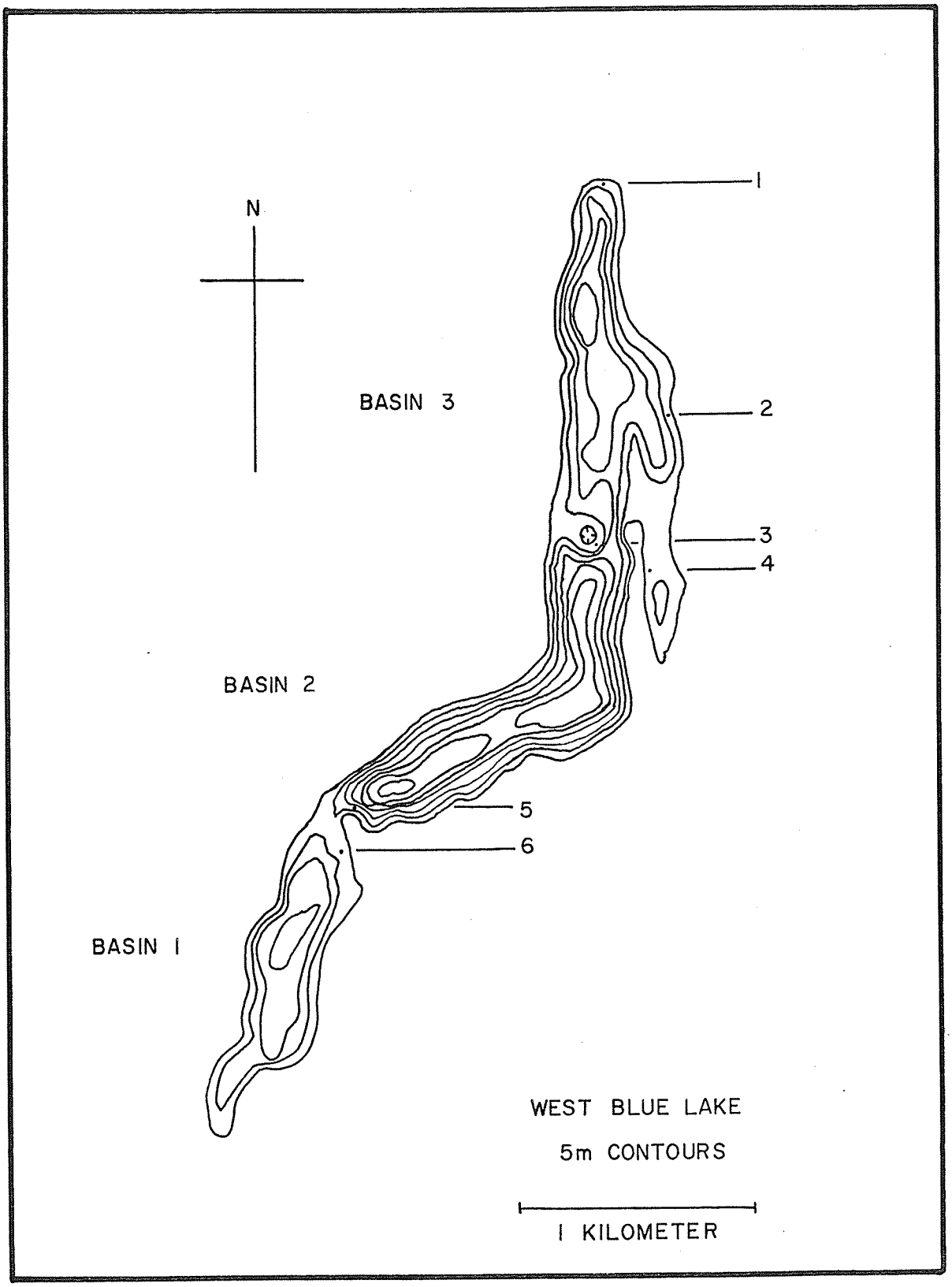

N
BASIN 3
BASIN 2
BASIN 1
1
2
3
4
5
6
WEST BLUE LAKE
5m CONTOURS
1 KILOMETER

Fig. 2 Seasonal changes of average daylengths for 1969; B. Seasonal changes of surface and average (0 - 20 m) water temperatures for 1969 and 1970.

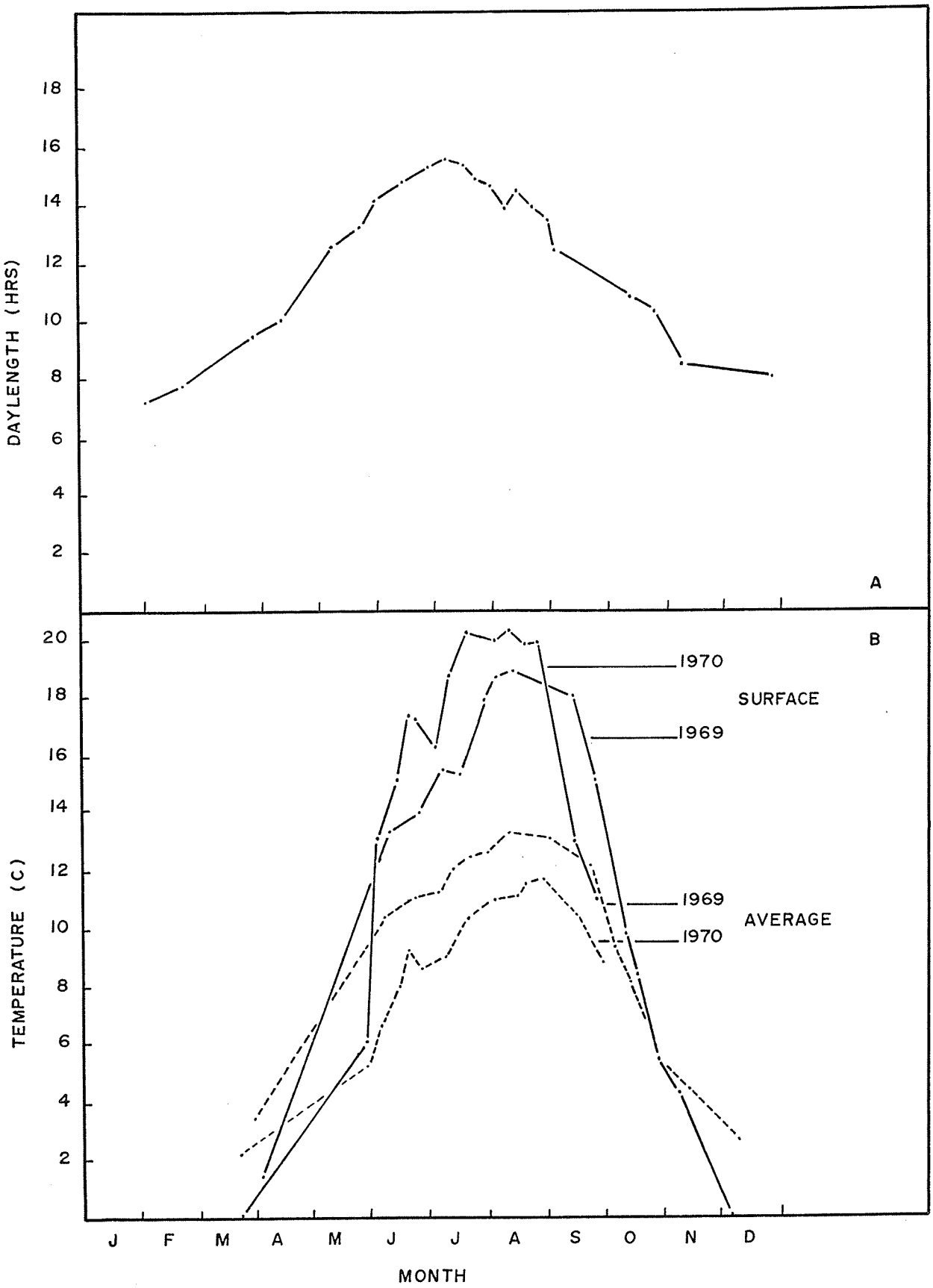
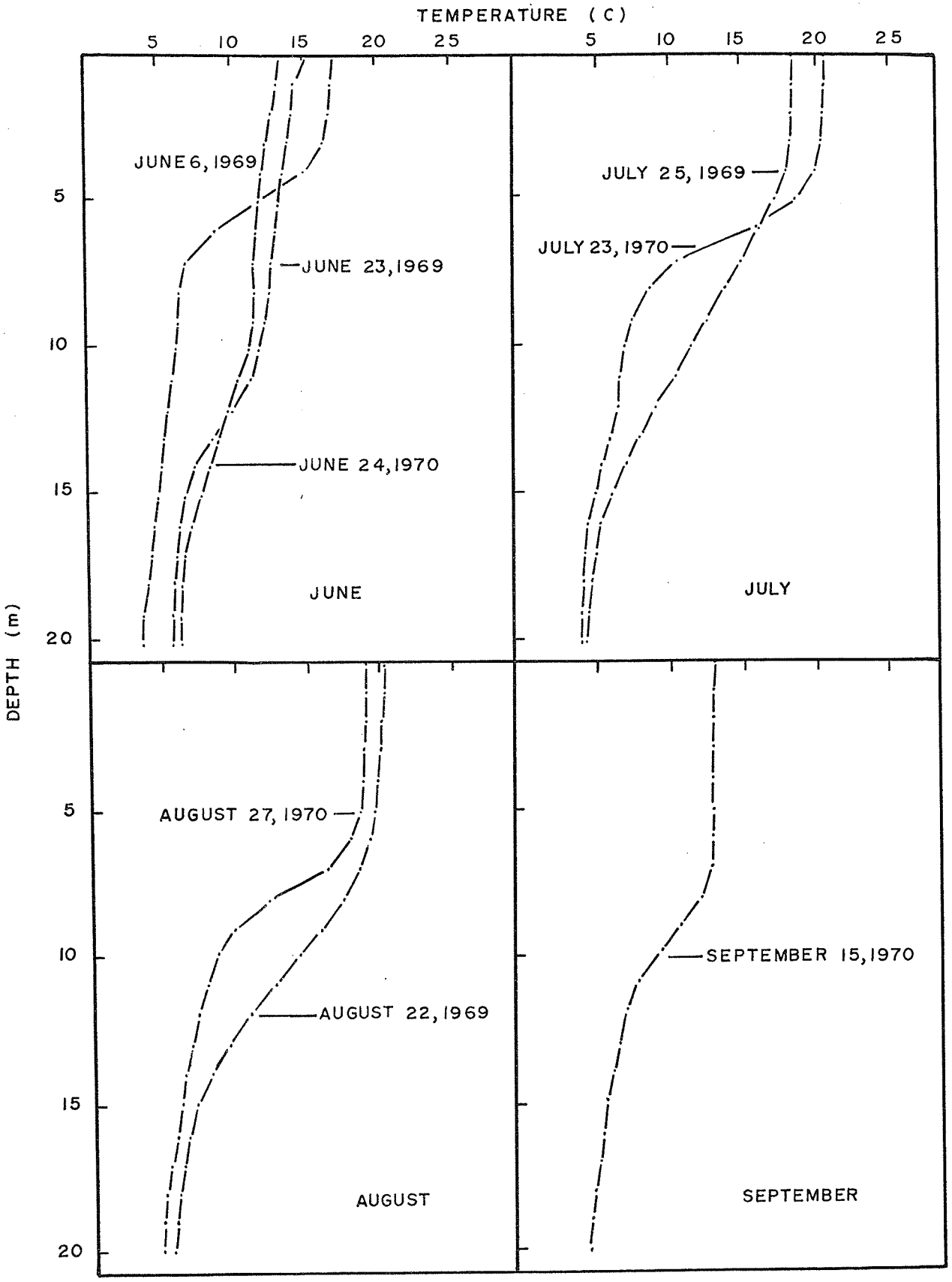

DAYLENGTH (HRS)
18
16
14
12
10
8
6
4
2
A
B
TEMPERATURE (C)
20
18
16
14
12
10
8
6
4
2
1970
SURFACE
1969
1969
AVERAGE
1970
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

Fig. 3 Vertical temperature profiles for West Blue Lake during 1969 and 1970.


TEMPERATURE (C)
5
10
15
20
25
DEPTH (m)
5
10
15
20
JUNE 6, 1969
JUNE 23, 1969
JUNE 24, 1970
JUNE
JULY 25, 1969
JULY 23, 1970
JULY
AUGUST 27, 1970
AUGUST 22, 1969
AUGUST
SEPTEMBER 15, 1970
SEPTEMBER

Mollusca and immature aquatic insects which are too numerous to mention here. Walleye, Stizostedion vitreum vitreum, yellow perch, Perca fluviatilis flavescens, northern pike, Esox lucius and stickleback, Culaea inconstans, are the endemic fish species.

Principle hydrophytes are Chara sp, Ranunculus circinatus, Potamogeton pectinatus and Potamogeton richardsoni.

Sampling

Dates, locations and gear used in sampling yellow perch in West Blue Lake during the ice free periods of 1969 and 1970 are shown in Table 1. The food habits of large perch (adults) and small perch (juveniles) were studied in 1969 and 1970 respectively. For the most part, sampling was conducted monthly at previously selected locations (Fig. 1) which were assumed to be feeding areas because of the localized concentration of perch. Although sample locations were chosen for similarities in depth, aquatic vegetation and substrate, alternate locations were utilized if insufficient perch were caught or adverse climatic conditions prevailed. Gill nets, used in the collection of fish, were set at right angles to shore. This procedure was chosen since Hasler and Bardach (1949) reported that perch undergo onshore movements and feed while moving parallel to shore. Perch were not observed to regurgitate when they became entangled in gill nets.

Assumptions underlying the methods employed in this study are that perch were collected at random, that food in their stomachs was representative of the population, and that regurgitation was not appreciable.

Table 1. Dates, locations, substrates, depth and gear used in sampling yellow perch in West Blue Lake during 1969 and 1970. (G.N. = gill net; S.M. = stretched measure; N = nylon; M = monofiliament.)

Data	Location	Substrate	Depth (m)	Gear		
				Type	Length (m)	S.M.(mm)
June 8-9, 1969[1]	4	Mud	2-7	G.N.(N)	30.48	38.1
June 22, 1969[1]	3	Chara beds	1-10	G.N.(N)	30.48	38.1
				G.N.(M)	15.24	38.1
				G.N.(N)	30.48	50.8
July 23-24, 1969[1]	3	Chara beds	1-10	G.N.(N)	30.48	50.8
				G.N.(M)	15.24	38.1
August 24-25, 1969[1]	5	Chara beds	2-10	G.N.(N)	30.48	38.1
		Potamogeton		G.N.(N)	30.48	50.8
June 23-24, 1970[1]	3	Mud & Chara	1-10	G.N.(M)	15.24	19.1
		beds		G.N.(M)	15.24	25.4
July 21-22, 1970[1]	1	Ranunculus &	1-8	G.N.(M)	15.24	19.1
		Potamogeton		G.N.(M)	15.24	25.4
July 22, 1970	1	Ranunculus &	1-5	G.N.(M)	15.24	19.1
		Potamogeton	5-8	G.N.(M)	15.24	19.1
July 22, 1970	4	Chara beds	1-8	G.N.(M)	15.24	19.1
August 24-26, 1970[1]	1	Ranunculus &	1-8	G.N.(M)	15.24	19.1
		Potamogeton		G.N.(M)	15.24	25.4
September 14-16, 1970[1]	6	Chara &	1-8	G.N.(M)	15.24	19.1
		Potamogeton		G.N.(M)	15.24	25.4
September 16, 1970	1	Ranunculus &	1-8	G.N.(M)	15.24	19.1
		Potamogeton				

[1]Dates of diurnal nettings.

During 1969 and 1970 water temperatures and photoperiod data were collected by personnel at the West Blue Lake field station. Water temperatures were measured at regular intervals throughout the seasons by a battery operated (ARA texas) hydrographic thermometer (model number FT 3 MARINE). Both seasonal changes of water temperature and vertical profiles were determined. The average weekly day lengths were determined from the recording produced by a Belfort's pyroheliometer (model number 5-3850) by using critical values of fifteen minutes after sunrise and before sunset.

For each diurnal netting experiment gill nets were set at a location before sunrise. and fish were removed and counted at two hour intervals, until perch were no longer caught. If insufficient numbers of perch were caught during one day of netting, additional samples of perch were collected on subsequent days. If many perch were caught during a time interval only a fraction was used for stomach analysis but the total catch was recorded. Two hour intervals were sufficient, since few perch were caught during some intervals and digestion of food organisms during this period would not be great. Perch, removed from the net for stomach content analysis, were weighed to the nearest 0.1g using a top loading balance for small fish and a rough balance for larger fish, after being blotted dry. Total and fork lengths to the nearest mm below were determined using a fish measuring board. Sex was determined and

scales were removed. All data were recorded on scale envelopes. The entrails of larger perch were removed by dissection, and preserved in 5% of 40% formalin while small fish were preserved whole after being killed and their abdomens slit open.

Analysis

Subsequent food analysis, carried out on individual stomachs, consisted of determining the number and weight of the various food organisms present as well as arbitrary stages of digestion. Organisms were identified according to order, class, family or genus, depending upon the food organism, using keys in Pennak (1953) and Usinger (1963). Numbers of small partially digested food items were determined by counting head capsules (Diptera pupae) or eyes (Amphipoda and Cladocera). Weights were measured as blotted dry weight to the nearest mg on a single beam balance. Perch were grouped according to time of day and netting equipment so that diurnal and temporal changes in food habits could be determined. Additional groupings of juvenile perch were made to facilitate comparisons between locations and depths for the same date and between years. Stomach analysis carried out on these groups entailed calculating the percentage frequency of occurrence, numbers and weight of the various food items plus the percentage of empty stomachs. In addition, quantitative comparisons within and among netting experiments were carried out. This was accomplished by determining the mean quotients of total stomach weight divided by fish weight (Index of stomach fulness)

for each two hour time interval and the total sample including empty stomachs.

Chi-square analyses were carried out on the number of stomachs containing a particular food item compared to the total number of fish with stomach contents, among and between successive sampling dates, to detect temporal differences in the food organisms eaten. Similar analyses were performed between locations and depths. Grouping of food organisms was frequently necessary to increase the sample size. Chi-square was also used to test for significant differences between sampling dates for the number of empty stomachs.

The correlations of both the mean indices of fulness and percentage empty stomachs with water temperature and average daylength were calculated by Pearson's correlation analysis (Pearson and Lee, 1903) for each series of diurnal nettings.

Results of Bartlett's test (Snedecor and Cochran, 1968) indicated that the within sample variances of the diurnal netting experiments were not homogeneous ($P < 0.05$) and hence comparisons using the degree of stomach fulness were not valid using parametric statistical procedures. However, back transformed means and 95% confidence limits, including and excluding empty stomachs for each two hour period and the total sample, were determined from the square root transformation recommended by Bartlett (1947). Differences in the indices of fulness within and among sample dates were tested by the Kruskall-Wallis rank sum test and between dates by the Wilcoxon rank sum described by Siegel (1956). Friedman's test (Friedman, 1937) was used to determine whether the daily changes in catch

rate varied over the season for adult and juvenile perch.

Perch were also grouped according to fork length for each sample date to reveal differences in feeding habits with size. Analyses of these data consisted of determining the percentage occurrence and weight of major food items. Further analysis of feeding with size was performed on perch caught both in 1969 and 1970 grouped into two centimeter intervals. For each length interval the mean stomach content weight was determined. The natural logarithm of stomach content weight was related to the natural logarithm of perch length by the least squares method of linear regression (Snedecor and Cochran, 1968). The slope was tested by a t-test (Snedecor and Cochran, 1968) against an ideal equilibrium constant of 3.0 to determine if stomach content weight increased in direct proportion to fish weight. Perch in West Blue Lake were found to obey the cube law since the exponent in the equation $W = aL^n$, was 3.081.

Gastric Digestion Rates

Four experiments were conducted on adult perch and three on juvenile perch to determine digestion rates of natural food organisms. Experimental variables are summarized in Table 2. The method used for adult perch was the "Direct Estimation Method," (Windell, 1968) where depletion of the weight of stomach contents is equated to that of digestion. Perch were collected using 48.1 and 50.8 mm (stretched measure) nylon gill nets, the fins clipped for identification and the fish

Table 2. Dates, size of fish, food and temperatures for digestion rate experiments conducted on juvenile and adult yellow perch.

Date	No. of Perch	Size Range (mm)	Food		Temperature (C)
			Aliquot % of Body Weight	Type	
June 1969	20	178-220	0.52	Amphipods (*Gammarus lacustris*; *Hyalella azteca*)	11.5-13.5
July 1969	19	155-216	0.45	Amphipods (*Gammarus lacustris*; *Hyalella azteca*)	16.0
June 1970	10	135-182	1.21	Stickleback (*Culaea inconstans*)	15.0
June 1970	77	53-119	1.89	1	15.0
July 1970	12	151-203	1.74	Crayfish (*Orconectes virilis*)	20.0
July 1970	69	67-117	1.35	1	20.0
Sept. 1970	115	66-110	2.24	1	13.0

1. See qualitative analysis for 1970 in Fig. 12.

held in a covered 560 l fiberglass holding tank supplied with continuously flowing water at habitat temperatures. After a 72 hr starvation period to clear the gut, perch were force fed an aliquot of live food organisms of known number and weight. The method of feeding varied depending upon the food items. Amphipods were injected directly into the stomach by an injection force feeder, described by Dill (1969). Crayfish and sticklebacks were inserted into the esophagus using forceps, after which the perch voluntarily swallowed the meal. Individual fish were observed for approximately five minutes, to insure that regurgitation did not occur, then reintroduced into the 560 l tank. At intervals over the experimental period fish were removed, the stomach contents dissected out, blotted dry and weighed to the nearest mg. In addition the state of digestion was recorded. Finally, the weight of food remaining in the stomach was subtracted from the initial weight and expressed as a percentage of the initial weight. This percentage was used to indicate the degree of digestion and from graphs drawn by inspections the number of hours required for a 50 and 95 percent digestion was estimated.

The method employed for juvenile perch involved obtaining a large sample of fish using 19.1 and 25.4 mm (stretched measure) gill nets. Fish were then placed in aerated 27.4 l aquaria which were suspended in a covered 560 l holding tank supplied with continuously flowing water at habitat temperatures. Sub-samples (5-10 fish) were taken at the beginning and at intervals over the experimental period. The initial

sample was analysed for the percentage occurrence, numbers and weight of food organisms present, while results from subsequent samples were expressed as indices of fulness. The mean indices of fulness including fish with empty stomachs were plotted against time. Differences between the slopes of the relationships between the natural logarithms of the indices of fulness and time were tested by the analysis of covariance (Robson and Atkinson, 1960). The exponential equation described by Tyler (1970) was used to determine the instantaneous coefficients of depletion and the times to 50 and 95% digestion. The "Index of stomach fulness" was used instead of the actual stomach content weight in all calculations.

Daily Food Consumption

The average amount of food consumed per day, on a wet weight basis, by juvenile perch was estimated from knowledge of their diurnal changes in the degree of stomach fulness and their respective gastric digestion rates. Consumption was first calculated for each two hour interval and then summed over all time intervals to obtain daily consumption. The equation developed for this method is as follows:

$$C = \sum_{i=1}^{n} [(A_i + (b_i + b_{i-1})) - A_{i-1}] \times 100$$

where: C = daily consumption (% of body weight)

A = index of fulness at end of the i^{th} interval

A_{i-1} = index of fulness at start of the i^{th} interval

b_i = first derivative of b using A_i

b_{i-1} = first derivative of b using A_{i-1}

n = number of intervals

when: $[(A_i + (b_i + b_{i-1})) - A_{i-1}]$ is a negative quantity the interval consumption is taken to be 0.

The amount of food present in the stomach at the end of an interval (A_i) was considered to be the sum of the amount consumed during the interval (C_i), the amount present from the previous interval (A_{i-1}) and an imaginary amount which was digested during the interval ($b_i + b_{i-1}$). The average amount of food digested during the two hour time interval was estimated as the sum of the first derivatives of b for A_i and A_{i-1}. Interval consumption was then calculated by adding the amount present at the end of the interval (A_i) to the amount digested ($b_i + b_{i-1}$) and subtracting the amount from the previous interval (A_{i-1}). After summing the interval consumption values the daily consumption and multiplying by 100 daily consumption is expressed as a percentage of body weight. Finally, estimates of the daily consumption of individual food items were determined by multiplying their percentage, by weight in the diet by the total food consumption.

The estimate of average daily food consumption for August was calculated using the gastric digestion rate data for July since perch differed little in their food habits and water temperatures were similar both months. Several assumptions were made, upon which validity of this method rests. These are:

1) That perch exhibit a diurnal feeding pattern and do not feed at night.

2) That perch feed on or near areas designated as feeding grounds and do not differ greatly in their food habits in other regions of the lake.

3) That perch consume an average quantity during the day and that this quantity of food can be estimated by collecting fish at intervals over the feeding period.

4) That the results of digestion rate experiments are applicable under actual field conditions.

5) That an average rate of digestion can be determined for all food organisms.

Daily consumption was not estimated for adult perch since, due to peculiarities in their feeding habits and failure to meet the last three assumptions they did not lend themselves to any existing field method of estimation.

To determine if the results from the calculations of average daily consumption for juvenile perch were sufficient for growth (somatal and gonadal) the equation, $G = pR-T$ (Winberg, 1956), was used where:

G = energy of weight increase (cal /day)

p = correction for incomplete utilization of ration

R = energy of ration (cal/day)

T = energy of metabolism (cal/day)

The energy content of the ration (R) was determined by summing the relative energy contributions of the various food items present in the diet. Califoric values of food items in West Blue Lake were obtained from N. B. Snow and J. R. M. Kelso (pers. comm.). The correction for incomplete utilization of

the ration (p) was taken to be 0.8, which is that suggested by Winberg (1956). The energy of metabolism (T) was determined from the parabolic relationship between metabolism and weight,

$Q = \alpha W^{\gamma}$, were:

Q = rate of oxygen consumption (ml O_2/hour)

α = level of metabolism (ml O_2/g/hour)

W = weight of the fish (g)

γ = a constant (pure number)

the rate of oxygen consumption (Q) was determined for the average fish weight (W) from each diurnal netting experiment using the level of metabolism (α) equal to 0.3 a value for freshwater fish and 0.181, found for yearling perch both given by Winberg (1956) at 20 C. The two values of were corrected to both surface and average water temperature by Krogh's normal curve (Ege and Krogh, 1914) by conversion factors given by Winberg (1956) yielding four separate measures of Q for each netting experiment. The resting metabolism (Q) was then multiplied by 2.0 to estimate metabolism in nature (Winberg, 1956). Finally to obtain T the daily oxygen consumption (Q) was multiplied by 4.89 (Brody, 1945) to obtain the total energy of metabolism in calories per day.

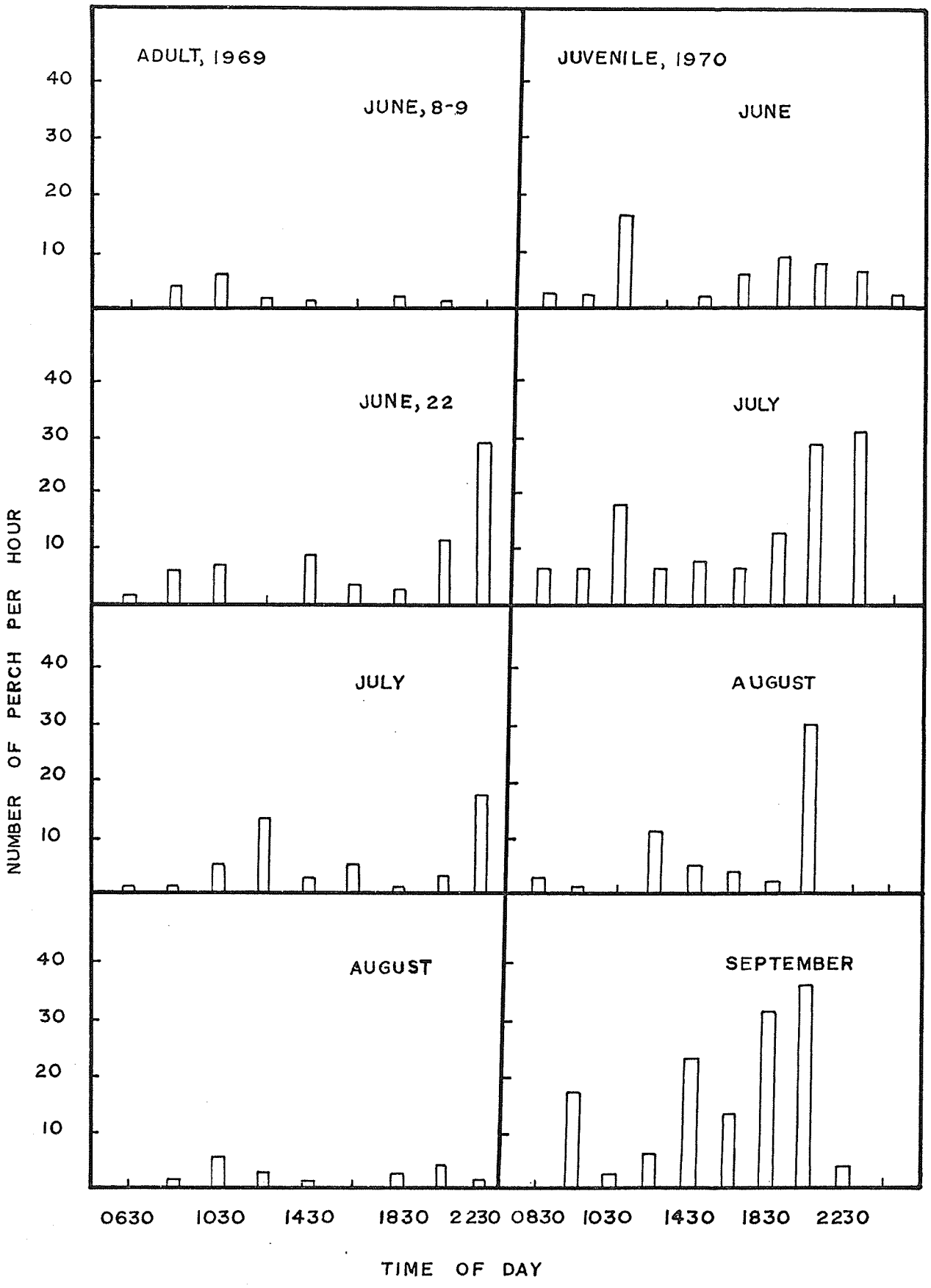
RESULTS

The order of presentation of the results obtained from this study is food habits, rates of gastric digestion, and estimates of average daily food consumption. Under these sections the food habits of adult and juvenile perch are given separately since they were obtained in different years. Food habits were analysed with respect to time of day, season and size of fish and are shown in that order. Rates of gastric digestion are presented before estimates of daily food consumption since they were used in determining the latter. First results pertaining to daily and seasonal catch rates are given.

Daily and Seasonal Catch Rates

Perch were found to be active only during the day with daily variation in the catch rate occurring among nettings (Fig. 4). In subsequent presentation of results and discussion daily changes of activity and feeding will be referred to as diurnal. In general, catch rates were somewhat bimodal with the greatest catch per unit effort in the evening. The hypothesis that catch rate did not differ significantly among netting experiments for both adult and juvenile perch was accepted when tested by Friedman's test. ($\chi^2 = 1.737,\ 8.015;\ P < 0.05$) The activity of perch increased after sunrise when walleye ceased to be caught in the nets but were not caught after dusk when walleye moved into the feeding grounds. No perch were

Fig. 4 Diurnal changes in capture rate for yellow perch during 1969 and 1970.


ADULT, 1969
JUVENILE, 1970
JUNE, 8-9
JUNE
JUNE, 22
JULY
JULY
AUGUST
AUGUST
SEPTEMBER
NUMBER OF PERCH PER HOUR
10
20
30
40
0630
1030
1430
1830
2230
0830
1030
1430
1830
2230
TIME OF DAY

caught after nightfall although extensive efforts were made with gill nets set at various locations and depths at night to catch them. Perch were observed to remain motionless on the bottom or among submergent vegetation when efforts were made to locate them in shallow water at night with a flashlight. Based on gill net catches, perch tended to inhabit deeper water in the morning and shallower water in the evening. Further, small perch tended to inhabit shallower water than larger perch.

Differences in catches over the season at the same location indicated that the relative abundance in areas varied. Additional evidence for changing area abundance was that streamer tags placed on perch by West Blue Lake personnel in previous years were recovered in different basins. Differences in the size composition of perch schools in the littoral regions over the season were observed. Schools composed of perch of all sizes were noted in spring and early summer while by late summer schools were largely composed of small sized individuals.

Diurnal Feeding Habits

Diurnal changes of stomach content weight expressed per unit of body weight (stomach fulness) for juvenile perch caught during 1970 are shown in Fig. 5. Variation in both the kinds of food items and of stomach fulness over the day were found to occur among months making separate treatment of the results necessary. In June, stomach fulness was greatest in the morning from 0830 to 1430 hrs, tapering off towards evening.

Fig. 5 Diurnal changes of the index of stomach fulness for juvenile perch caught during 1970. Vertical bars indicate the range. Numbers in parentheses are percentages of empty stomachs. Horizontal lines below time axes indicate time periods in qualitative comparisons.

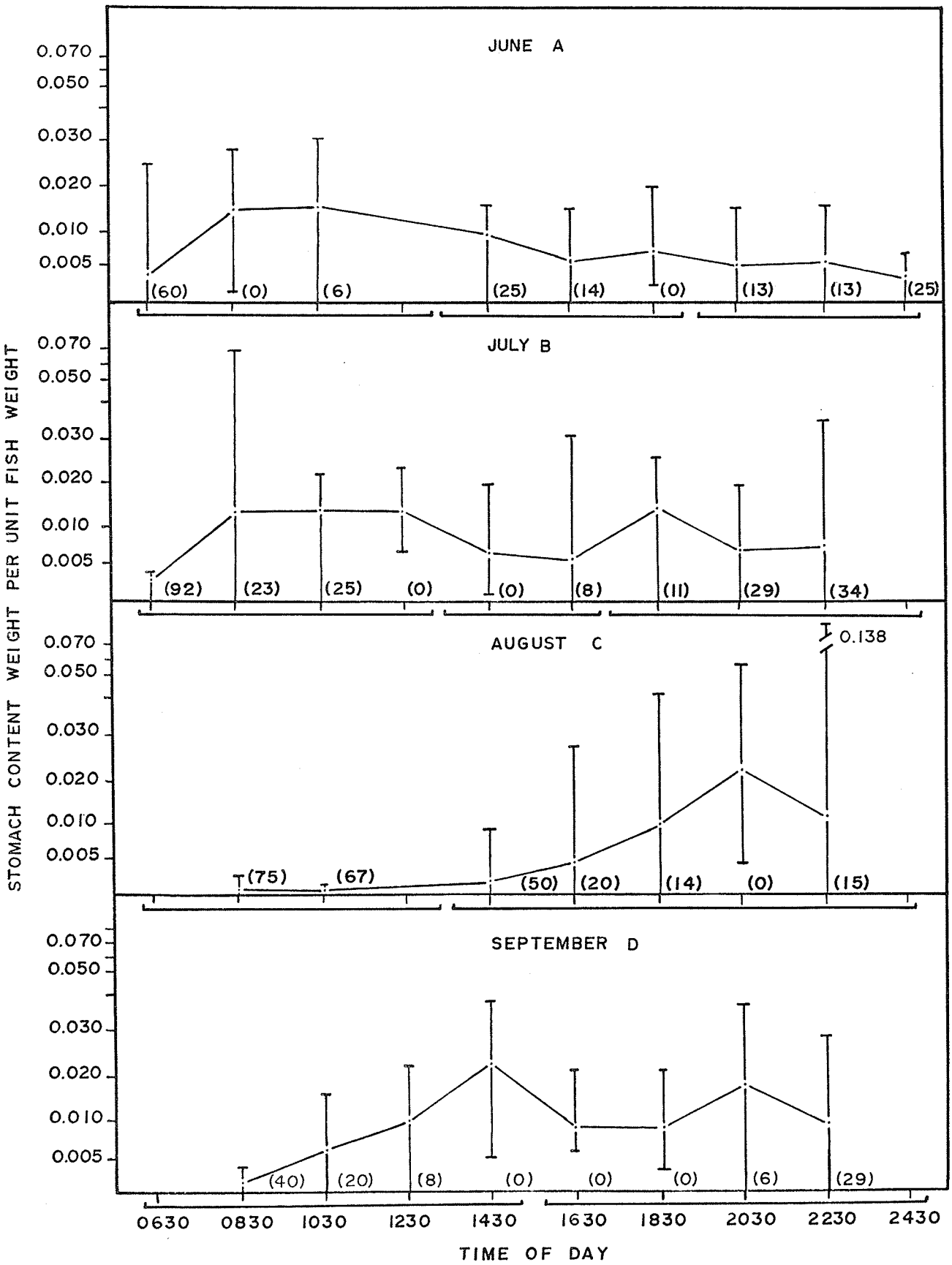
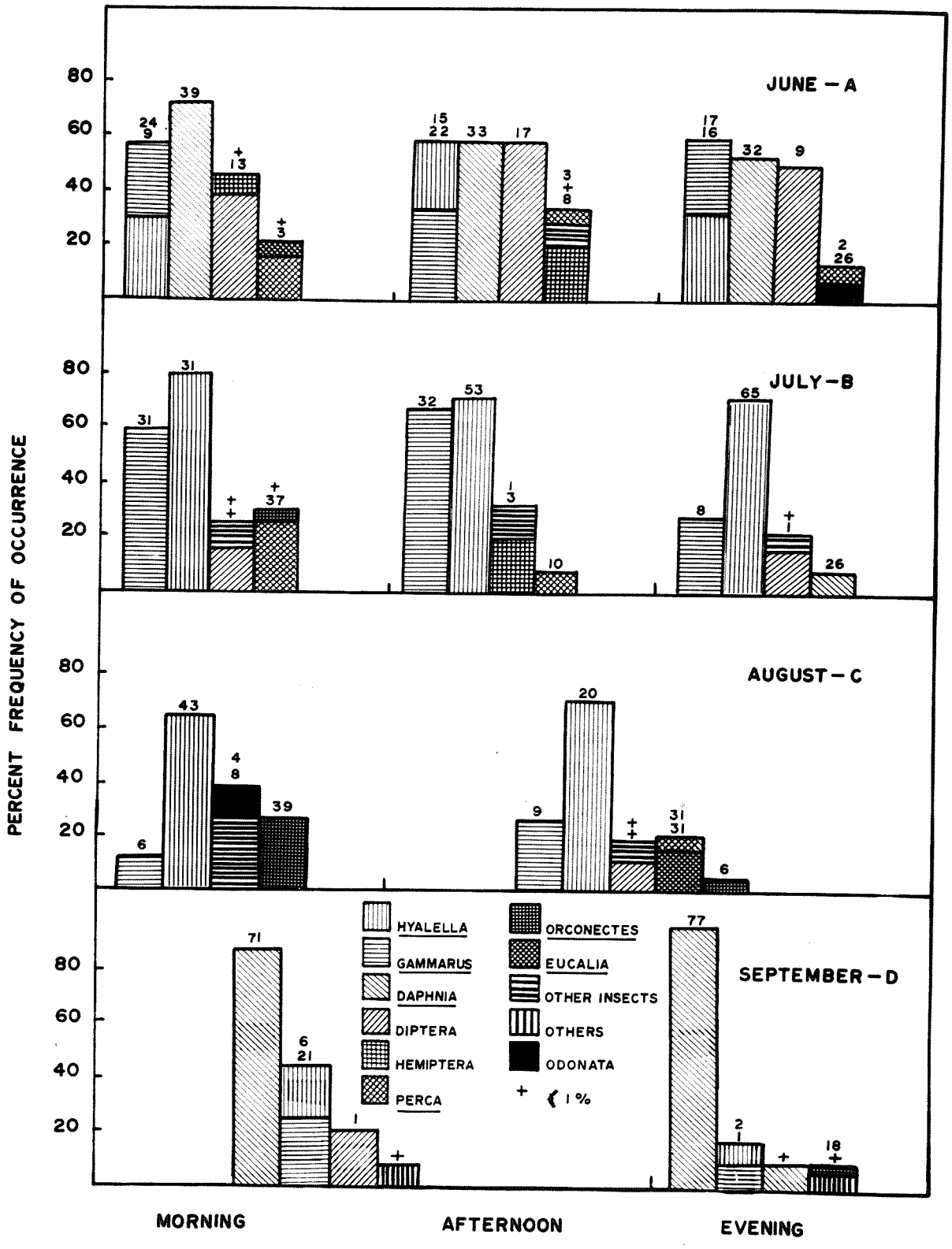

JUNE A
JULY B
AUGUST C
SEPTEMBER D
STOMACH CONTENT WEIGHT PER UNIT FISH WEIGHT
0.070
0.050
0.030
0.020
0.010
0.005
(60) (0) (6) (25) (14) (0) (13) (13) (25)
(92) (23) (25) (0) (0) (8) (11) (29) (34)
0.138
(75) (67) (50) (20) (14) (0) (15)
(40) (20) (8) (0) (0) (0) (6) (29)
0630 0830 1030 1230 1430 1630 1830 2030 2230 2430
TIME OF DAY

Fig. 6 Percentage occurrence of major food items in juvenile perch stomachs for time periods within 1970 diurnal netting experiments. Numbers above rectangles are the percentage by weight.


PERCENT FREQUENCY OF OCCURRENCE
JUNE – A
JULY – B
AUGUST – C
SEPTEMBER – D
HYALELLA
GAMMARUS
DAPHNIA
DIPTERA
HEMIPTERA
PERCA
ORCONECTES
EUCALIA
OTHER INSECTS
OTHERS
ODONATA
+ < 1 %
MORNING
AFTERNOON
EVENING

Changes in the degree of stomach fulness for July showed a bimodal pattern with a broad peak at 0830 to 1230 hrs and an abrupt, but higher, peak at 1830 hrs. In contrast stomach fulness was the greatest at 1830 and the morning values were substantially lower than those for June and July. In September a bimodal pattern for stomach fulness was again evident with peaks occurring at 1430 and 2030 hrs.

In June cladocerans, amphipods and immature diptera were found in the stomachs of perch throughout the day and showed little fluctuation in weight (Fig. 6-A). Other insects and fish were present in relatively few perch stomachs during the day and did not constitute a major portion of the diet. The percentage of perch with empty stomachs was low during the morning and early evening.

Amphipods were found in the majority of perch stomachs during the July netting (Fig. 6-B). Occurrence of Hyalella in the diet remained constant over the day but increased in percent by weight. Gammarus occurred in fewer stomachs in the evening and decreased in percent by weight. Immature diptera were found only in the morning and evening periods. Other insects, crayfish and fish were present in a minority of perch stomachs with small perch comprising the greatest bulk of the diet in the morning. The percentage of perch with empty stomachs was high in the morning, low during midday, when all perch stomachs contained food, but increased towards evening.

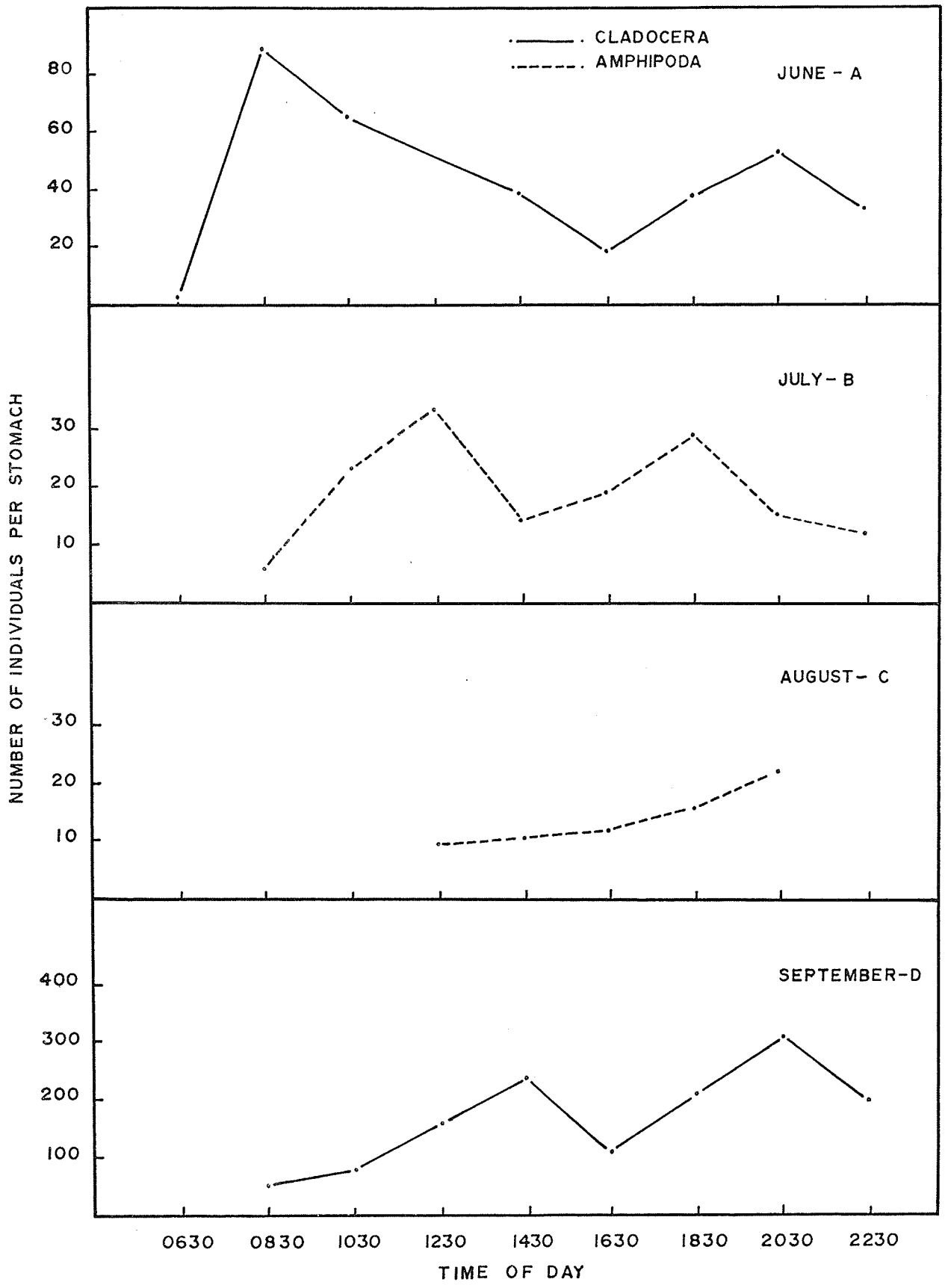
In August, (Fig. 6-C), amphipods were found in most

stomachs during both periods. The percentage of perch feeding on insects was greater in the morning. Crayfish formed 39% by weight of the diet in the morning and 6% in the evening while fish formed 62% by weight of the food in the evening and did not occur in the stomach during the morning period. The percentage of perch with empty stomachs was generally the reciprical of the degree of stomach fulness.

Cladocerans formed the basic food items present in perch stomachs during both periods for September and constituted the greatest bulk of the diet (Fig. 6-D). Amphipods occurred more frequently as food items in the morning when they comprised a significant portion of the diet. Insects, crayfish and fish were found infrequently in stomachs during both periods and did not make up an appreciable segment of the diet. The percentage of perch with empty stomach contents decreased to mid-day when all stomachs contained food then increased in the evening.

To determine if peak periods of stomach fulness were actually peak feeding periods, the average numbers of food items present in perch stomachs during each time interval of the diurnal nettings were determined (Fig. 7). Only food organisms which were eaten in sufficient numbers to facilitate comparisons were used and gave a better indication of the time of feeding activity than larger food items which were digested slowly and eaten infrequently. In June the average number of cladocerans per stomach (Fig. 7-A) was greatest at the start of the morning peak of stomach fulness (Fig. 5-A)

Fig. 7 Diurnal changes of the average numbers of small food items found in juvenile perch stomachs.


CLADOCERA
AMPHIPODA
JUNE - A
JULY - B
AUGUST - C
SEPTEMBER-D
NUMBER OF INDIVIDUALS PER STOMACH
80
60
40
20
30
20
10
30
20
10
400
300
200
100
0630
0830
1030
1230
1430
1630
1830
2030
2230
TIME OF DAY

and rose again in the evening. The average number of amphipods increased to 1230 hrs in July (Fig. 7-B) corresponding to the end of the morning peak of stomach fulness (Fig. 5-B). Amphipods rose again at 1830 hrs corresponding to the evening peak of stomach fulness. In August the average number of amphipods per stomach (Fig. 7-C) increased in relation to stomach fulness (Fig. 5-C). Finally the average number of cladocerans per stomach in September showed peaks at 1430 and 2030 hrs (Fig. 7-D) which occurred at the same time of peak stomach fulness (Fig. 5-D).

For adult perch collected during 1969, each netting could be divided into three periods based on the degree of stomach fulness (Fig. 8). These were: 1) a morning period when stomach contents were maximal; 2) an afternoon period when stomach contents were low and 3) an evening period when stomach fulness increased again but not to the morning level. The percentage of perch with empty stomachs was lowest in the morning and evening periods. Peak periods of stomach fulness may not be interpreted as peak feeding periods without information concerning the sample size and digested state of the food organisms. In many cases peak periods of stomach fulness may be explained by individual fish which recently consumed large food organisms or by the presence of partially digested food items which were eaten the previous day.

From the first diurnal netting experiment (June 8-9) amphipods and immature diptera were present in perch stomachs throughout the day (Fig. 9-A). The percentage by weight of

Fig. 8 Diurnal changes of the index of stomach fulness for adult perch caught during 1969. Vertical bars indicate the range. Numbers in parentheses are percentages of empty stomachs. Horizontal lines below time axes indicate the periods used in qualitative comparisons.

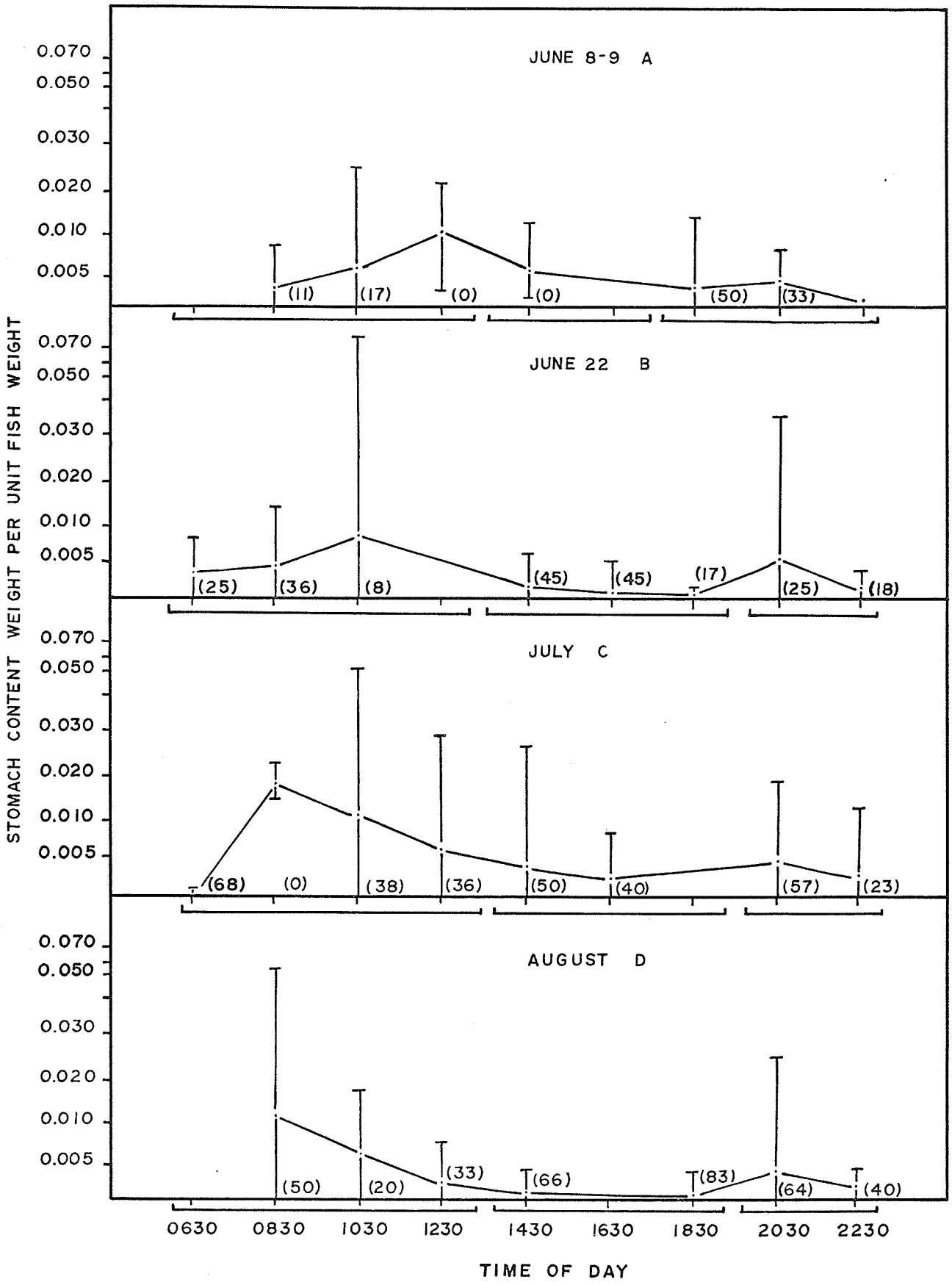
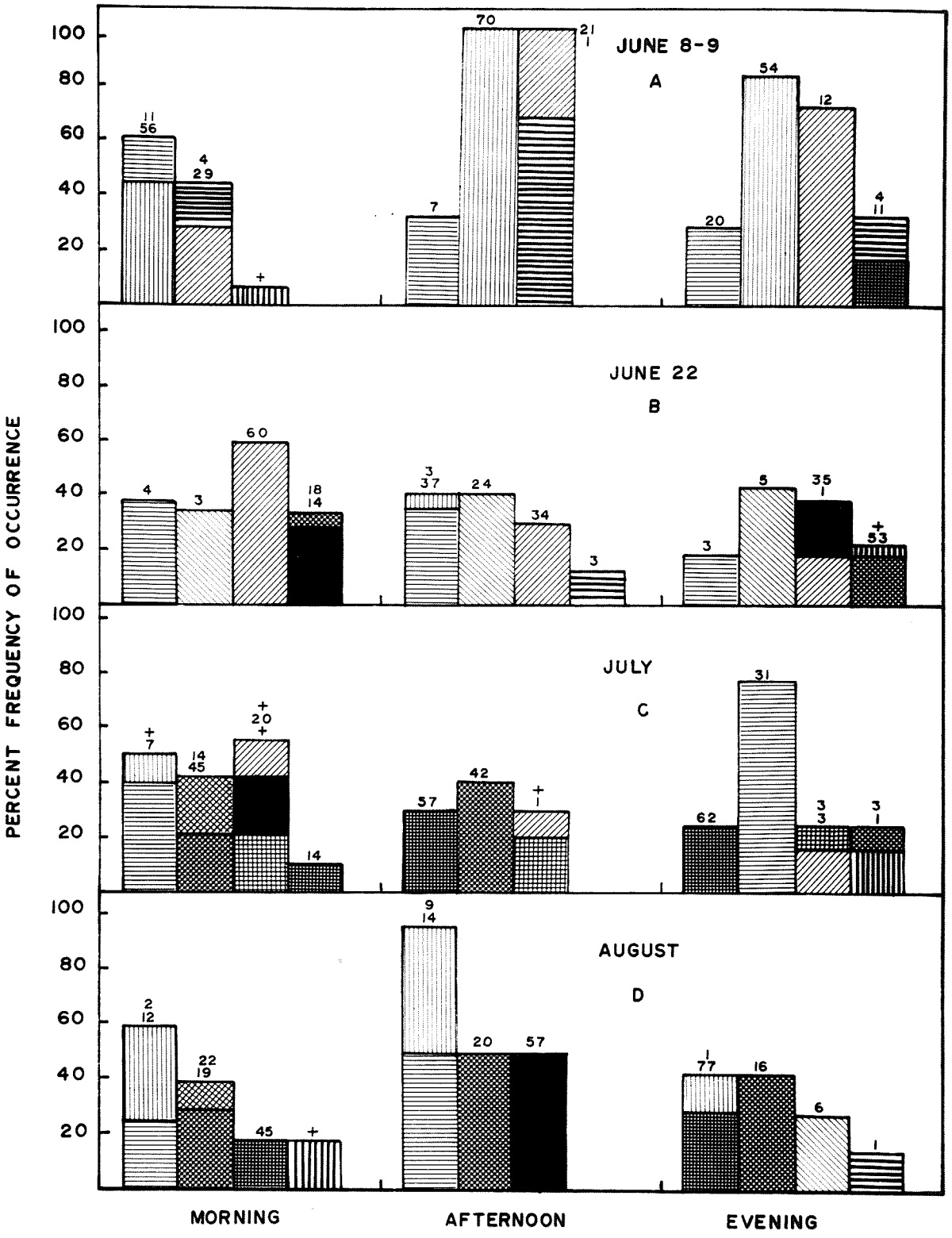

JUNE 8-9 A
JUNE 22 B
JULY C
AUGUST D
STOMACH CONTENT WEIGHT PER UNIT FISH WEIGHT
0.070
0.050
0.030
0.020
0.010
0.005
(11) (17) (0) (0) (50) (33)
(25) (36) (8) (45) (45) (17) (25) (18)
(68) (0) (38) (36) (50) (40) (57) (23)
(50) (20) (33) (66) (83) (64) (40)
0630 0830 1030 1230 1430 1630 1830 2030 2230
TIME OF DAY

Fig. 9 Percentage occurrence of major food items in adult perch stomachs for various time periods within the 1969 diurnal netting experiments. (See Fig. 6) Numbers above rectangles indicate the percentage by weight.


PERCENT FREQUENCY OF OCCURRENCE
100
80
60
40
20
JUNE 8-9
A
JUNE 22
B
JULY
C
AUGUST
D
MORNING
AFTERNOON
EVENING

amphipods remained relatively constant while that of diptera decreased. Other insects and crayfish were incidental as food items and did not constitute a significant fraction of the diet by weight. The state of digestion of food organisms in the morning suggested that they were recently consumed while most of those present in the evening were in an advanced state of digestion.

In late June (Fig. 9-B) cladocerans, amphipods and immature diptera were found in the majority of perch stomachs throughout the day. The occurrence of cladocerans, expressed as a percentage, increased over the day but only constituted a significant portion of the diet by weight in the afternoon. Dipterans decreased in relative weight (66 to 1%) throughout the day and amphipods formed the greatest percent by weight of the diet in the afternoon. Other insects, fish and crayfish were incidental as food items and occurred largely in the morning and evening. The morning peak of stomach fulness (Fig. 8-B) may be exaggerated by the stomach contents of one large perch which had recently consumed a large number of Chaoborus pupae while the evening peak caused by food items which had been recently ingested.

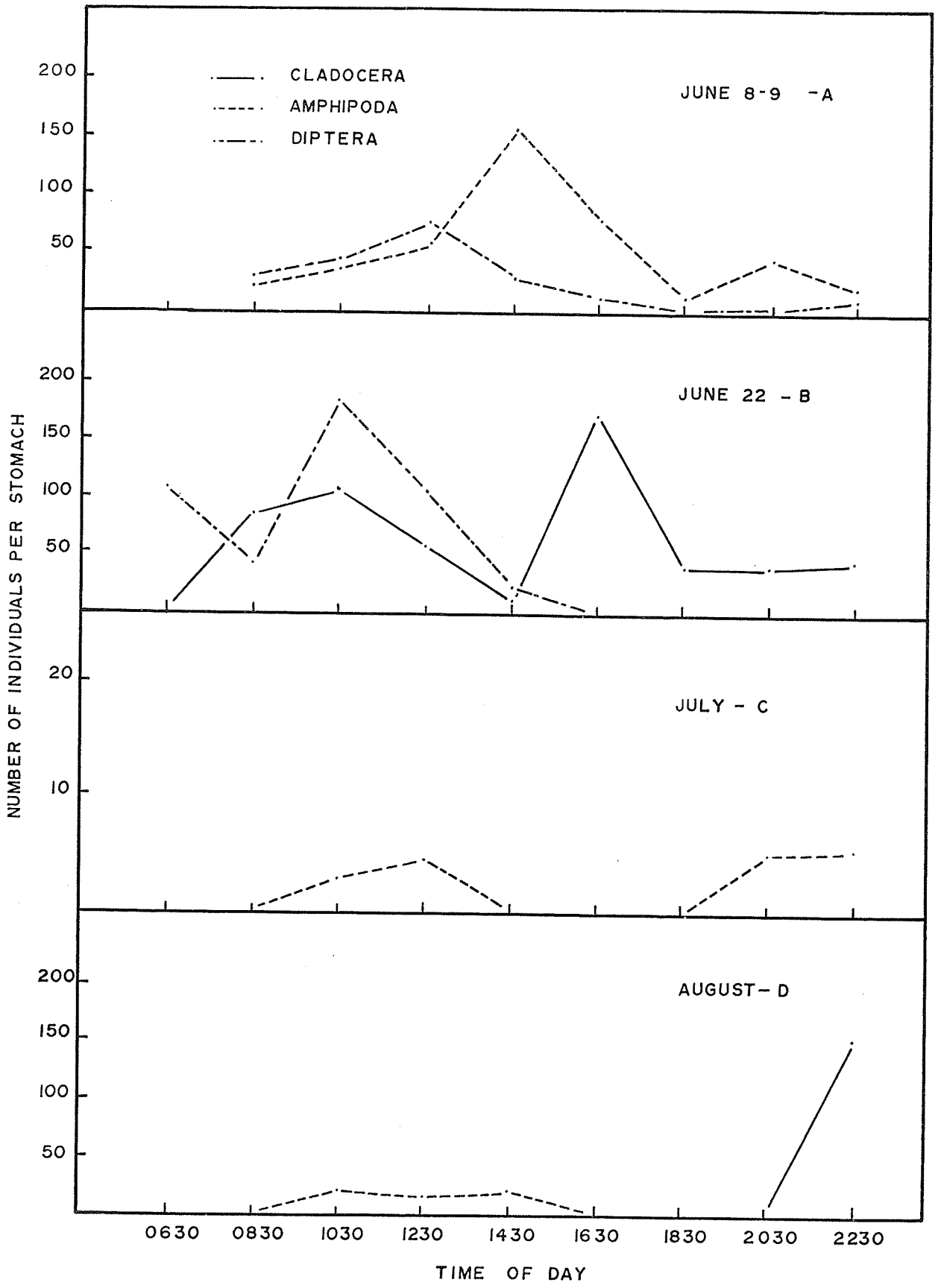
In July (Fig. 9-C) amphipods were most frequent but were only present in the morning and evening. Crayfish and fish were secondary in occurrence, and were present in stomachs throughout the day. Insects and snails were found infrequently in perch stomachs over the day with water-boatmen as the most frequently occurring insect. The morning peak of stomach ful-

ness (Fig. 8-C) was caused by a small number of perch which had recently consumed fish in their stomachs. The evening peak may be exaggerated by the presence of crayfish, consumed during the previous day, in several perch stomachs.

Amphipods were consumed by the greatest percentage of perch during the August netting (Fig. 9-D) but their presence in the diet was largely restricted to the morning and afternoon periods. Fish, present in perch stomachs throughout the day, decreased in weight relative to other food items from 41 to 16%. Crayfish were found in perch stomachs in the morning and evening when they respectively constituted 45 and 77% of the diet by weight. Insects were present in the majority of the stomachs in the afternoon when Odonata predominated. Cladocerans were only eaten in the evening. The morning period of stomach fulness (Fig. 8-D) may be explained by the presence of crayfish and fish which were consumed during the previous day. Conversely, the state of digestion of food items forming the evening peak suggested that they had been recently consumed.

Diurnal changes in the average number of small food items present in adult perch stomachs are shown for each netting experiment in Fig. 10. For June 8-9 the average number of immature dipterans reached a maximum at 1230 hrs, corresponding to the morning peak of stomach fulness (Fig. 8-A), then decreased. Amphipods showed one peak in numbers at 1430 hrs and a second peak 2030 hrs which coincided with the evening peak of stomach fulness. For June 22 the average numbers of both cladocerans and immature dipterans were greatest during

Fig. 10 Diurnal changes of the average number of small food items found in adult perch stomachs during 1969.


CLADOCERA
AMPHIPODA
DIPTERA
JUNE 8-9 -A
JUNE 22 - B
JULY - C
AUGUST - D
200
150
100
50
20
10
NUMBER OF INDIVIDUALS PER STOMACH
0630
0830
1030
1230
1430
1630
1830
2030
2230
TIME OF DAY

the morning and evening peaks of stomach fulness (Fig. 8-B). A second peak in cladocerans was evident at 1630 hrs but numbers leveled off during the peak period of stomach fulness (1830-2230 hrs). The average number of amphipods per stomach was greatest after the morning peaks of stomach fulness in both July and August (Fig. 8-C and D). In July, amphipods increased in numbers coinciding with the evening peak of stomach fulness (Fig. 8-D).

With the exception of the diurnal experiment on juvenile perch collected in August 1970, the daily changes of stomach fulness showed a bimodal pattern. Results of the Kruskal-Wallis rank sum test among the two hour time intervals from the diurnal netting experiments were not significant for adult perch collected in early June and August 1969 (χ^2 = 5.366, 7.219; $P > 0.05$) whereas all other comparisons were significant. This suggests that the observed diurnal changes in stomach fulness for juvenile perch collected during 1970 were a result of actual differences in the degree of stomach fulness while those for adult perch could be due to chance.

Observed changes in the degree of stomach fulness over the day did not correspond to either the timing of sunrise or sunset or to catch rates of adult and juvenile perch.

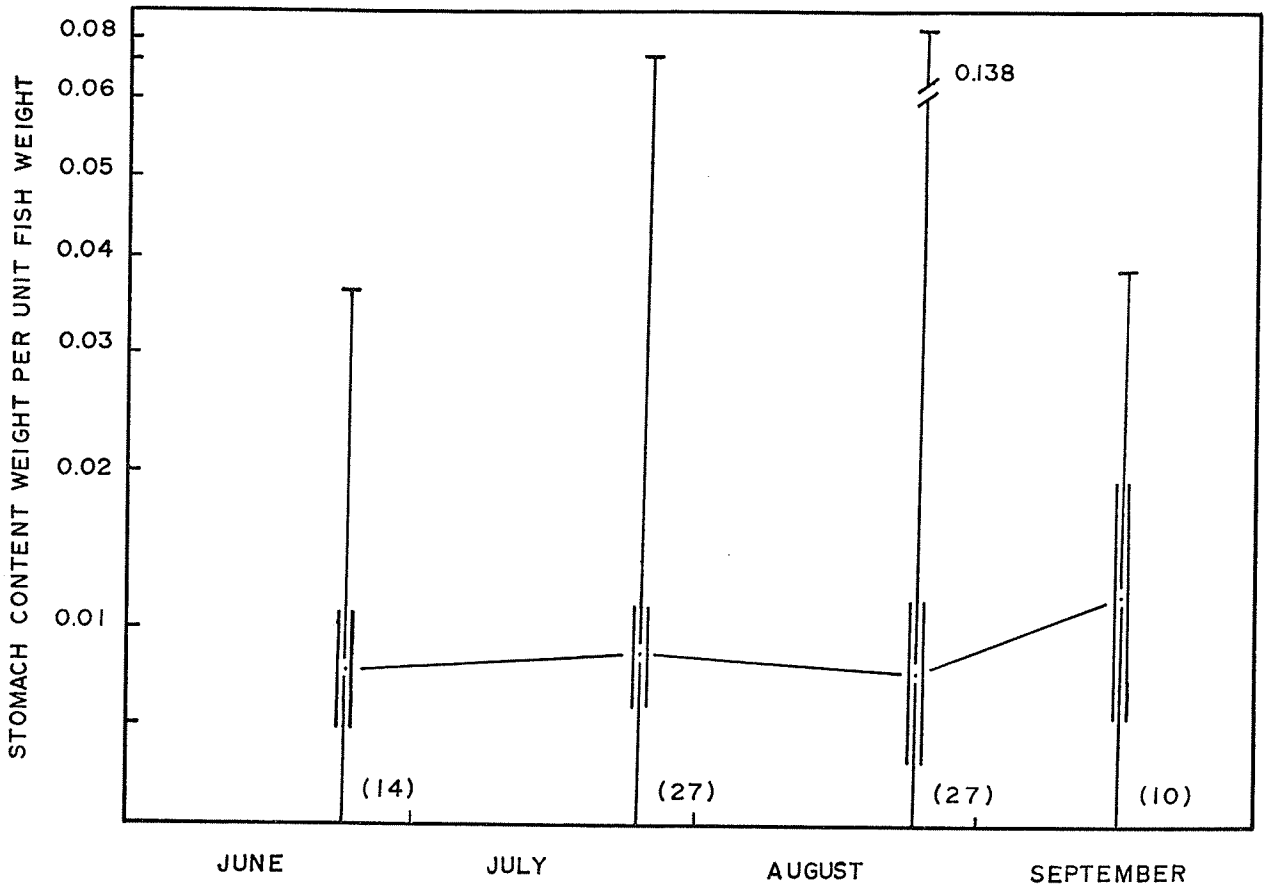
Food items were found in various stages of digestion throughout the day but were identifiable and could be counted. It was noted that individual fish fed on particular organisms with variation in the diet largely occurring among groups of perch. If large food items were consumed (crayfish, fish,

dragonfly nymphs) they did not eat other food items unless the initial food was in an advanced state of digestion. Similarly cladocerans, amphipods and immature aquatic insects tended to comprise the diet of individual perch. Other food organisms occurred infrequently in stomachs, either comprising the stomach contents or a small fraction of the total diet.

Temporal Feeding Habits

Seasonal changes occurred in mean stomach content weight per juvenile perch weight and in the frequency of occurrence of perch with stomach contents. (Fig. 11). Stomach fulness increased from June to July, decreased in August and then increased in September when the mean value was the highest. The hypothesis that there was not a significant difference among sampling dates for degree of stomach fulness was rejected. The chi-square value obtained using the Kruskall-Wallis rank sum test was 23.913 ($P < 0.05$). Results of the Wilcoxon rank sum test showed significant differences ($P < 0.05$ to occur only between August and each of June, July and September plus between September and July where the "Z" values were 2.596, 2.105, 3.745 and 3.599 respectively. The percentage of juvenile perch with empty stomachs increased from June to August then decreased in September. Chi-square values for the number of empty stomachs were found to be statistically significant between August and both of June and September plus between July and September ($\chi^2_c = 10.004, 6.117, 7.452$; $P < 0.05$).

Fig. 11 Seasonal changes of mean stomach content weight per unit fish weight for juvenile perch during 1970. Percentage of empty stomachs in parentheses. Vertical bars indicate the range; parallel bars indicate confidence intervals (P = 0.95).


STOMACH CONTENT WEIGHT PER UNIT FISH WEIGHT
0.08
0.06
0.05
0.04
0.03
0.02
0.01
0.138
(14)
(27)
(27)
(10)
JUNE
JULY
AUGUST
SEPTEMBER

perch varied seasonally (Fig. 12). For instance, cladocerans were eaten by the majority of perch in June and September when they constituted 32 and 69% by weight of the diet but were absent in July and August. Amphipods, however, were taken as food items in June, but also in July and August when they constituted a 69 and 30% by weight of the food items eaten. Insects were eaten by perch throughout the season but were only of relative importance by bulk in June when perch fed heavily on immature diptera. Perch consumed fish throughout the season but while they occurred infrequently in the stomachs, the contributions in terms of weight was significant in July and August (39 and 60% of the total weight of stomach contents respectively). Crayfish were taken infrequently as food items during the season and were of relatively minor importance to the diet.

Results of chi-square tests among and between successive months for the occurrence of food items in juvenile perch stomachs are presented in Table 3. The hypothesis that there were no significant differences among months was rejected for all food organisms ($P < 0.05$). However, both significant and non-significant results were obtained between successive months. For example, the occurrence of amphipods in juvenile perch stomachs was statistically different for comparisons between June and July and between August and September ($\chi^2_c = 8.638$ and 18.050; $P < 0.05$) while not different for the comparison between July and August ($\chi^2_c = 0.280$; $P > 0.05$). The occurrence of fish in perch stomachs was significant only between

Fig. 12 Seasonal changes of the percentage occurrence of major food items in juvenile perch stomachs during 1970. Numbers above rectangles indicate the percentage by weight.

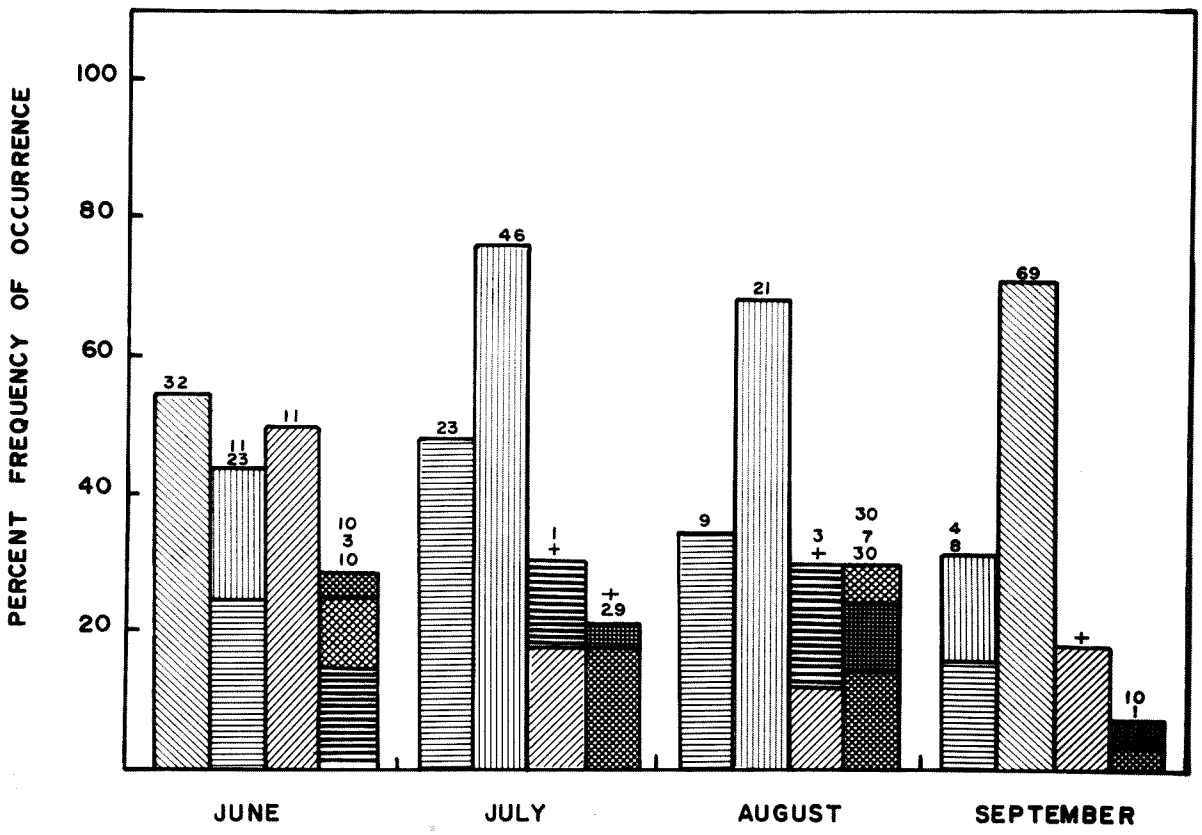

PERCENT FREQUENCY OF OCCURRENCE
100
80
60
40
20
32
11
23
11
10
3
10
23
46
1
+
+
29
9
21
3
+
30
7
30
4
8
69
+
10
1
JUNE
JULY
AUGUST
SEPTEMBER

Table 3. Results of chi-square analysis designed to test for significant differences among and between months for the occurrence of major food organisms in juvenile yellow perch stomachs, 1970. Among months χ^2 (P = 0.05; 3 df) = 7.81 and between months χ^2_c (P = 0.05; df = 1) = 3.84. (June (I); July (II); August (III); September (IV).

Food Organisms	χ^2 among months	χ^2_c between months		
		I-II	II-III	III-IV
Amphipods	33.575*	8.638*	0.280	18.050*
Gammarus	11.767*	4.326*	0.817	2.918
Hyalella	46.727*	16.329*	0.250	18.906*
Cladocera	104.463*	50.839*	N.C.	41.200*
Crayfish	7.814*	0.286	1.354	1.350
Fish	8.264*	0.320	0.026	5.610*
Sticklebacks	17.164*	1.821	11.224*	3.692
Perch	18.225*	1.001	6.123*	0.015
Insects	16.250*	4.567*	0.413	0.406
Diptera	22.194*	11.980*	0.344	0.639

N.C. = No comparison.

* = $P < 0.05$

August and September (χ^2_c = 5.610; $P < 0.05$) while significant differences for insects was found to occur only between June and July (χ^2_c = 11.980; $P < 0.05$). Despite the significant chi-square value for comparisons among months, the values between successive months were not significantly different.

Seasonal changes in mean stomach content weight per unit adult perch weight and in the frequency of occurrence of perch with stomach contents occurred (Fig. 13). The degree of stomach fulness decreased during June, increased again in July but decreased in August. The hypothesis that there was not a significant difference among sampling dates for the degree of stomach fulness was rejected. The chi-square value obtained from the Kruskal-Wallis rank sum test was 19.273 ($P < 0.05$). Based on results using the Wilcoxon rank sum test the hypothesis that there was no significant differences among sampling periods for the degree of stomach fulness was rejected for comparisons between June 8-9 and both of June 22 and August plus between June 22 and July (respectively Z = 2.091, 2.467, 4.429; $P<0.05$). The percentage of perch with empty stomachs decreased from June to August. Chi-square, used to test the hypothesis that there were no significant differences between months, were significant for comparisons between August and both of June 8-9 and June 22 (χ^2_c = 6.061, 3.948; $P < 0.05$).

There were seasonal changes in the occurrence and weight of major food organisms in adult perch stomachs occurred (Fig. 14). For instance, cladocerans were eaten by adult perch only in late June and August, and constituted only 6 and 2% respectively

Fig. 13 Seasonal changes of mean stomach content weight per unit fish weight for adult perch during 1969. Numbers in parentheses are percentages of empty stomachs. Vertical bars indicate the range; parallel bars indicate confidence intervals (P = 0.95).

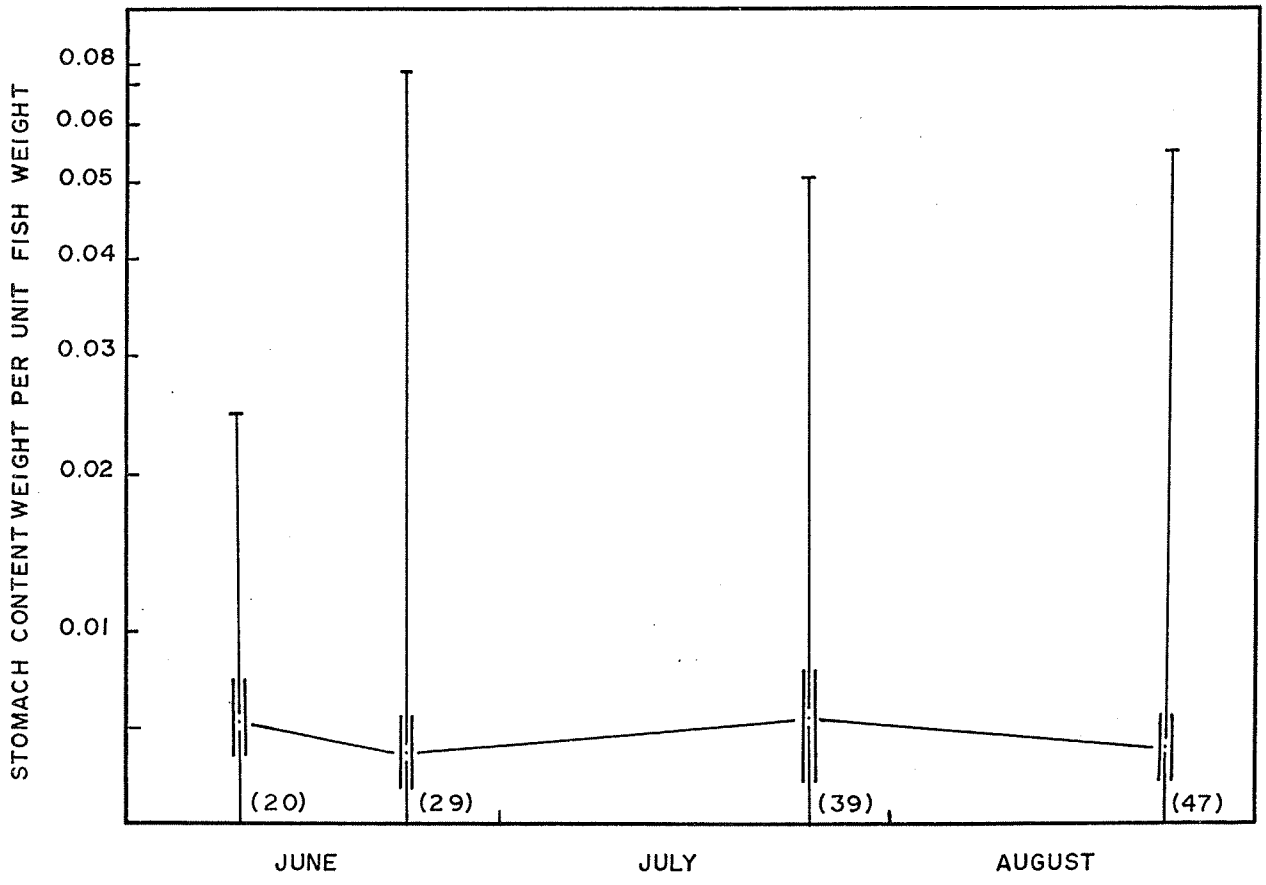
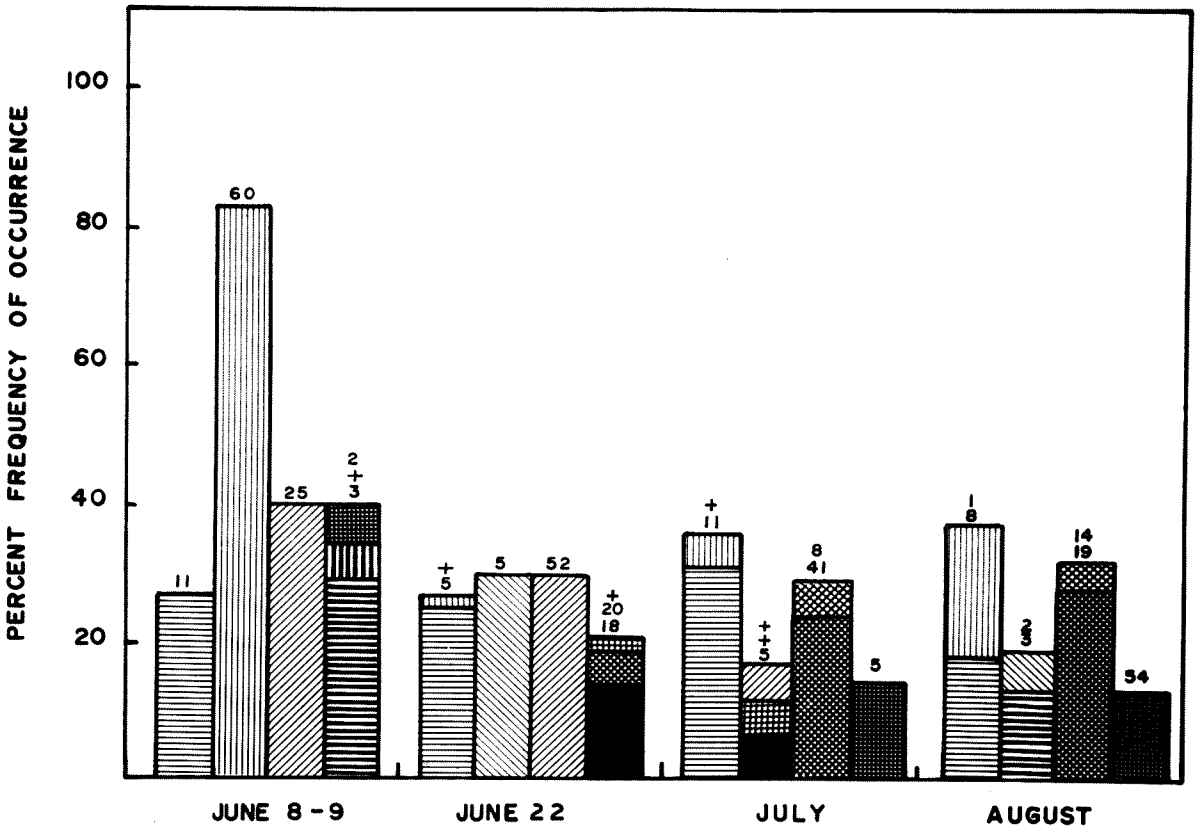

STOMACH CONTENT WEIGHT PER UNIT FISH WEIGHT
0.08
0.06
0.05
0.04
0.03
0.02
0.01
(20)
(29)
(39)
(47)
JUNE
JULY
AUGUST

Fig. 14 Seasonal changes in the percentage occurrence of major food items in adult perch stomachs during 1969. Numbers above rectangles are percentages by weight.


PERCENT FREQUENCY OF OCCURRENCE
100
80
60
40
20
11
60
25
2
+
3
+
5
5
52
+
20
18
+
11
+
+
5
8
41
5
1
8
2
3
14
19
54
JUNE 8 - 9
JUNE 22
JULY
AUGUST

of the diet by weight. Insects were consumed by most perch in June when immature dipterans comprised 52% of the diet by weight, but were of decreased importance in July and August. Amphipods were taken as food by most adult perch over the season, but only constituted an important food item in early June when they made up 71% by weight of the diet. The consumption of fish and crayfish by adult perch increased over the summer. The percentage by weight in the diet reached 49 and 84% respectively for fish in July and crayfish in August.

Results of chi-square tests, among and between successive months, for the occurrence of food items in adult perch stomachs are shown in Table 4. The hypothesis that there were no significant differences among months was rejected for all food organisms except Gammarus where $P < 0.05$. However, both significant and non-significant results were found to occur between successive months. For example, the occurrence of amphipods in perch stomachs was only significantly different between June 8-9 and June 22 ($\chi^2_c = 11.235$; $P < 0.05$). The occurrence of dipterans, fish and crayfish in adult perch stomachs was only significantly different between June 22 and July ($\chi^2_c =$ 7.093, 9.564, 5.191; $P < 0.05$). Despite the significant result obtained from comparisons among months for other insects no significant differences were observed to occur between successive months.

For both adult and juvenile perch the range of stomach content weight to fish weight ratio was much greater than the 0.95 confidence limits.

Table 4. Results of chi-square analysis designed to test for significant differences among and between successive months for the occurrence of major food organisms in adult yellow perch stomachs, 1969. Among months χ^2 (P = 0.05; 3 df) = 7.81 and between months χ^2_c (P = 0.05; 1 df) = 3.84. (June 8-9 (I); June 22[c](II); July (III); August (IV).

Food Organisms	χ^2 among months	χ^2_c between months		
		I-II	II-III	III-IV
Amphipods	14.728*	11.235*	0.103	0.004
Gammarus	1.547	-	-	-
Hyalella	68.846*	41.380*	0.075	5.005*
Cladocera	28.489*	8.054*	14.707*	2.017
Crayfish	10.229	0.482	5.191*	0.125
Fish	24.411*	0.592	9.564*	0.269
Stickleback	17.140*	0.592	5.231*	0.300
Perch	8.310*	N.C.	4.000*	0.017
Insects	10.550*	1.227	1.432	0.472
Diptera	19.900*	1.011	7.093*	0.0002

N.C. = No comparison

* = $P < 0.05$

The variation may be attributed to different levels of daily feeding activity and diversity of the food items eaten. The mean values of stomach fulness may be considered as underestimates of actual values since an uncertain fraction of perch may have been collected prior to feeding and after feeding with partially digested food remains in their stomachs. As previously mentioned food items were found in adult perch stomachs which, as judged by their state of digestion, were consumed prior to the netting experiment. The percentage by weight consumed during days prior to sampling increased from early June when all food items were eaten during the sampling date to August when 32% of the diet (crayfish and fish) were eaten on days previous (Table 5). In contrast, it

Table 5. Summary of average stomach content weight per fish weight from 1969 diurnal nettings for: 1) all perch; 2) perch with stomach contents); 3) perch with food consumed during the netting period; and 4) perch with food consumed prior to the netting period.

Date	No. of Perch	% Empty Stomachs	% of stom. wt. from previous days	Stomach content wt. per fish wt.			
				1	2	3	4
June 8-9	40	22.6	0.0	0.00542	0.00700	0.00700	0.0
June 22	87	28.7	0.5	0.00348	0.00493	0.00490	0.00003
July	71	39.4	24.4	0.00536	0.00885	0.00673	0.00212
August	51	47.1	31.6	0.00360	0.00681	0.00466	0.00212

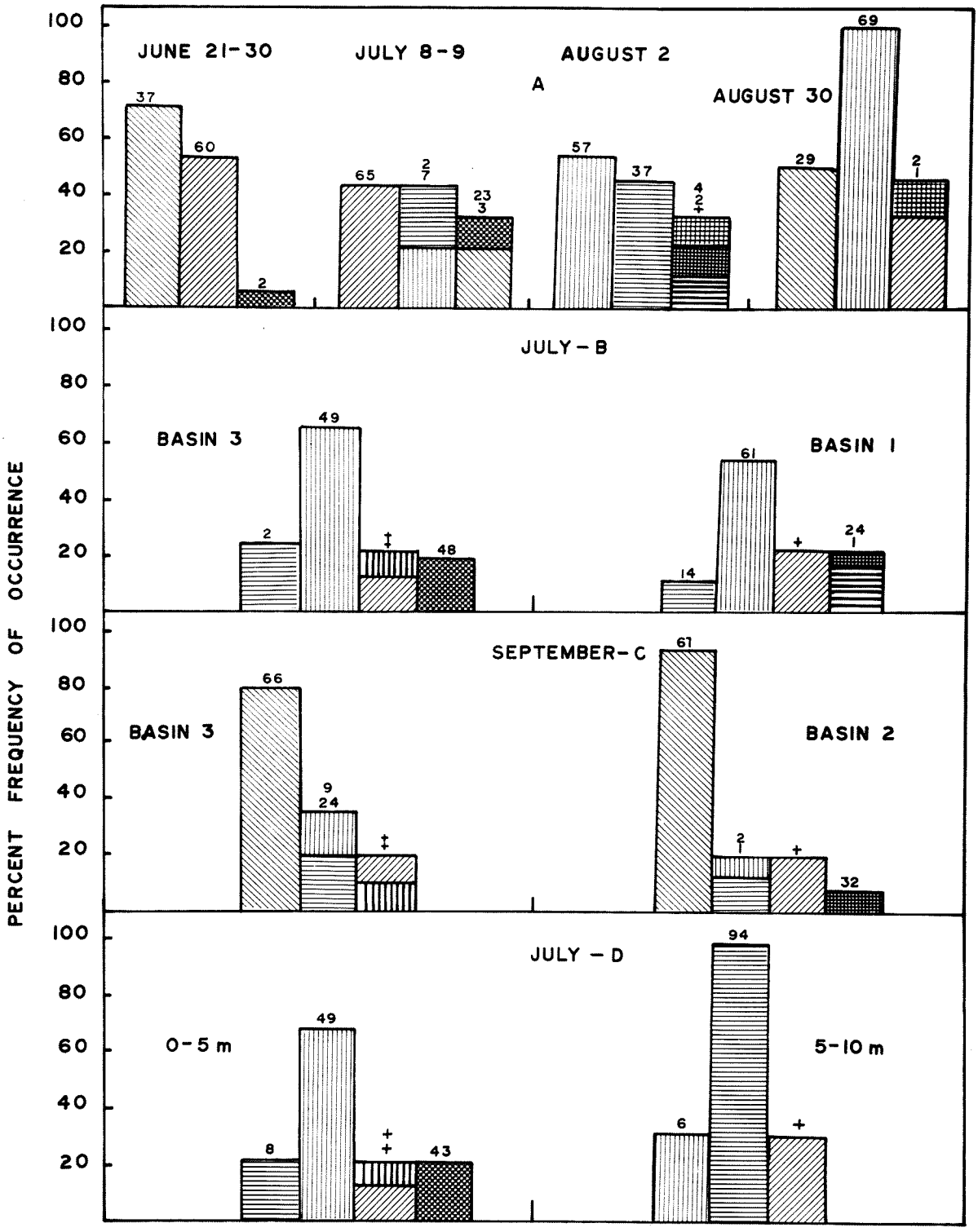
was observed that food items in juvenile perch stomachs were, for the most part, those which were eaten during the day of sampling. In July, the digested remains of one crayfish and in August the partially digested remains of one perch were found. The weight of these food organisms constituted less than one per cent of the total.

Results of simple correlation analysis showed that changes in the percentage of adult perch with empty stomach over the season was significantly correlated with both water temperature and average daylength (respectively $r_s = 0.9824$, 0.9871; $P < 0.05$) while stomach fulness showed no correlation with either temperature or average daylength. Although not significant ($P > 0.05$) seasonal changes of the percentage of juvenile perch with empty stomachs were directly related to water temperature and average daylength while the change in stomach fulness was inversely related.

Comparisons of Perch Food Habits Between Years, Locations and Depths

Similarities and differences in juvenile perch diet were found in both 1969 and 1970 (Fig. 12 and 15-A) but because samples were small in 1969 only the major components can be compared. In perch caught during June, cladocerans and immature dipterans were eaten in similar proportions while amphipods were absent from the 1969 sample. Most perch caught in early July, 1969 had eaten immature dipterans and to a lesser extent cladocerans while most perch from late July 1970 had eaten amphipods and no stomachs contained cladocerans. The

Fig. 15 Percentage occurrence of major food items in juvenile perch stomachs during 1969 (A). Comparisons of food habits between locations (B and C) and depths (D) for juvenile perch during 1970. Numbers above rectangles are percentages by weight.


PERCENT FREQUENCY OF OCCURRENCE
100
80
60
40
20
JUNE 21-30
JULY 8-9
AUGUST 2
AUGUST 30
A
37
60
2
65
2
7
23
3
57
37
4
2
+
29
69
2
1
JULY - B
BASIN 3
2
49
+
48
BASIN 1
14
61
+
24
1
SEPTEMBER - C
BASIN 3
66
9
24
+
BASIN 2
61
2
1
+
32
JULY - D
0-5 m
8
49
+
+
43
5-10 m
6
94
+

proportions of perch feeding on amphipods, immature insects and crayfish were similar in both years for early August 1969, and mid-August 1970. Food items eaten by perch in late August 1969, were similar to those of perch from early September 1970, when perch consumed cladocerans, amphipods and immature dipterans but the relative percentages differed.

In July 1970, the proportion of juvenile perch feeding on Hyalella, Gammarus and immature dipterans in Basin III, where the dominant vegetation was Potamogeton and Ranunculus, and Basin I, (Fig. 1), where the dominant vegetation was Chara, were similar (Fig. 15-B). Differences were only evident for the food items eaten by relatively few perch such as crayfish and fish. In September, the proportion of perch feeding on cladocerans, amphipods and immature dipterans were similar in Basin II and III where the dominant vegetation in both locations was Chara and Potamogeton (Fig. 15-C). Results of chi-square analysis designed to test the hypothesis that there were no differences in the occurrence of food items in perch stomachs between locations were not significant ($P > 0.05$). This suggests that the minor differences in the proportion of perch feeding on various food items could be explained by chance and not realized as actual differences between locations.

Two comparisons between areas for adult perch food habits were carried out during 1969 but analysis was done on pooled samples rather than individual fish. For this reason only comparisons of the individual food items can be made. In June the percentage contribution to the diet of 15 perch sampled

in Basin I for amphipods, crayfish, dipterans, other insects and fish were 18, 23, 9, 14 and 51% respectively. These results compare favourably with those collected in at the same time in Basin II for the diurnal netting experiment (Fig. 14). However, cladocerans were absent from the Basin I sample. In August the percentage contribution to the diet of 17 perch collected in Basin III for cladocerans, amphipods, crayfish, insects and fish was 1, 43, 14, 10 and 29% respectively. This again does not differ greatly from the results at the same time for the diurnal netting experiment (Fig. 16). Any apparent differences could be explained by the smaller sample sizes where variation may be expected to be great. Of interest here is that the major components of the diet were represented in both samples and in approximately the same proportions.

The results of stomach analysis carried out on juvenile perch, 1970, caught at different depths are shown in Fig. 15-D. Perch caught between 0 and 5m fed mainly on Hyalella and to a lesser extent on Gammarus and sticklebacks. In contrast, perch caught between 5 and 10m fed largely on Gammarus and to a lesser extent on Hyalella and immature dipterans. Despite these observed differences the result of chi-square tests failed to reject the hypothesis that there were no differences in the food items eaten at different depths ($P > 0.05$). This suggests that the observed differences may be explained by chance but the small sample sizes may render the test insensitive.

Relationship Between Feeding and Size

Stomach content weight increased per unit increase of fish length to the power of 2.366. The result of a t-test, used to determine if the observed increase was in direct proportion to fish weight by comparing the calculated exponent to an ideal exponent of 3.0, was significant ($t = 2.418$; $P < 0.05$; 13df). This implies that stomach content weight increases with fish length and hence fish weight but not in direct proportion to the latter. In other words, larger fish on the average have proportionately less in their stomachs than smaller perch. For example, from the equation in Fig. 16 a perch 70 mm in length (4.1 g) would have an average stomach content weight of 0.0525 (95% C.I. $\pm$ 0.0442) and the ratio of stomach content weight to fish weight of 0.0128. In contrast a perch 190 mm in length (90.6 g) would have an average stomach content weight of 0.510 g (95% C.I. $\pm$ 0.0449) and a ratio of 0.0056. Further, these ratios correspond well to the degree of stomach fulness in Fig. 9 and 11 respectively for juvenile and adult perch.

Since the kinds of food organisms consumed by perch varied among months and possibly between years, an analysis of the food habits with respect to fish size was done for each netting experiment. The percentage occurrence and weight of major food items eaten by juvenile perch during 1970, grouped into one cm length intervals for those in which sufficient numbers of perch were sampled, are shown in Fig. 17.

Fig. 16 Relationship between stomach content weight and fork length for all perch with stomach contents collected during 1969 and 1970.

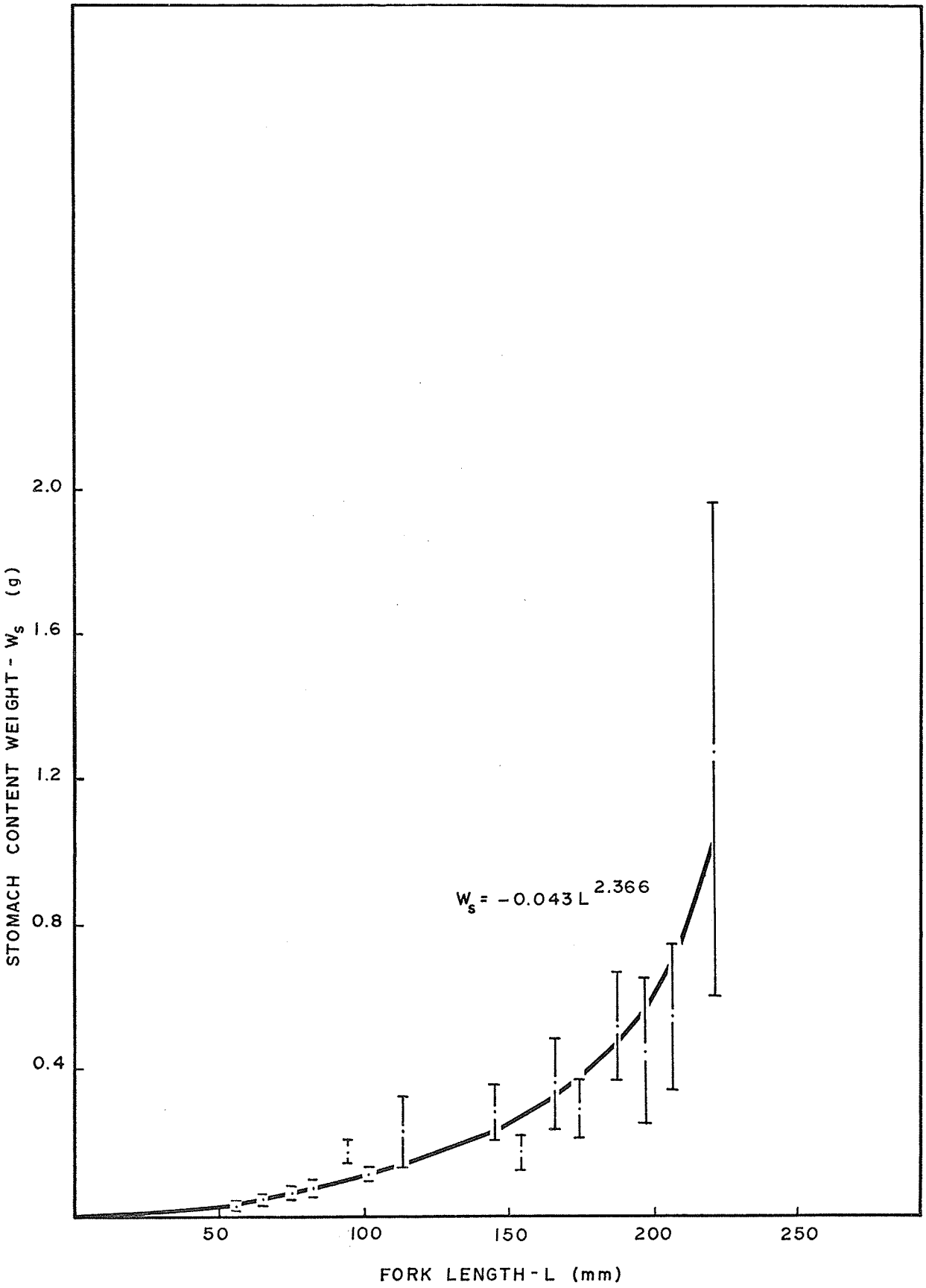
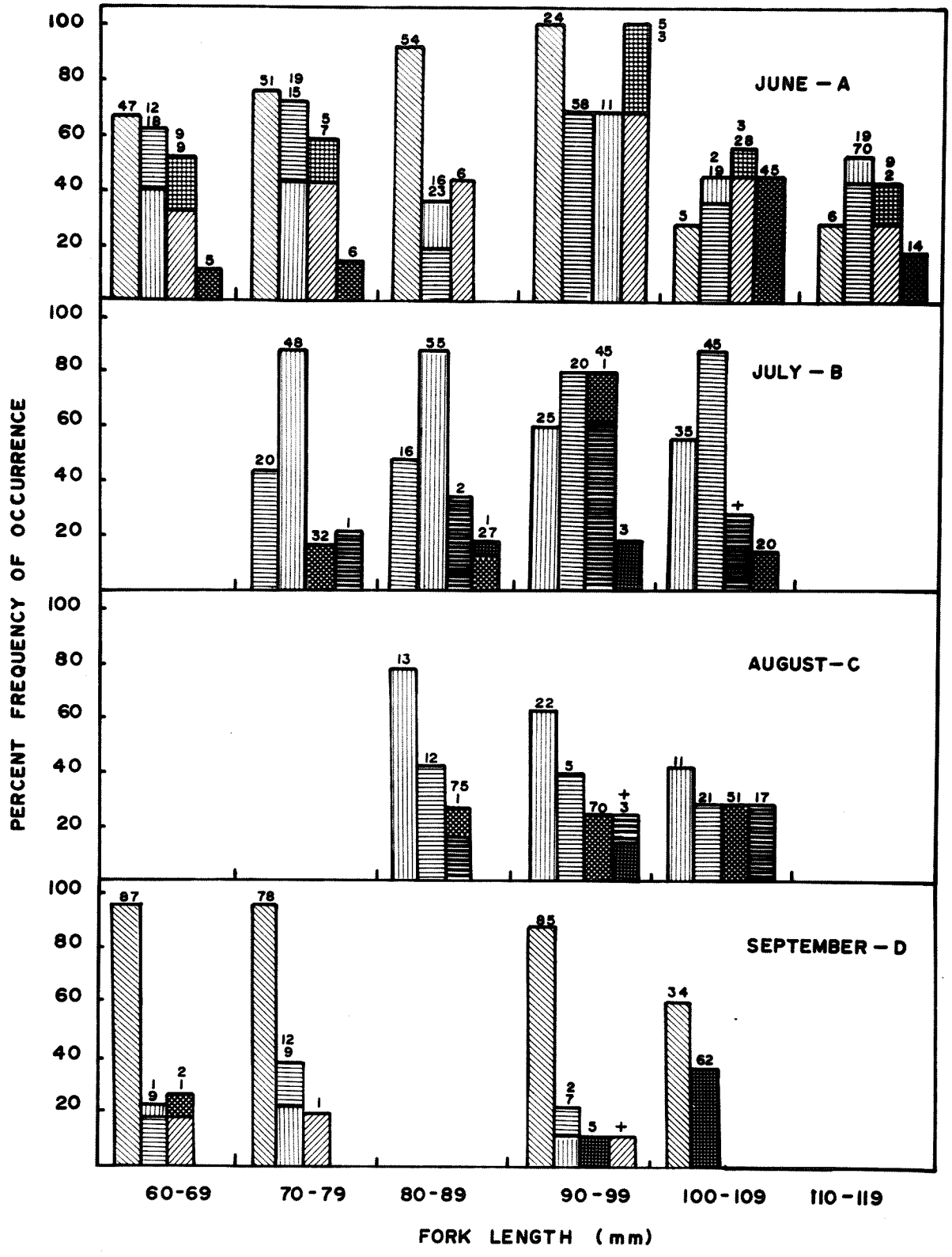

STOMACH CONTENT WEIGHT - W_s (g)
2.0
1.6
1.2
0.8
0.4
$W_s = -0.043 L^{2.366}$
50
100
150
200
250
FORK LENGTH - L (mm)

Fig. 17 Changes in the percentage occurrence of major food items with size of juvenile perch collected during 1970 diurnal netting experiments. Numbers above rectangles indicate percentages by weight.


JUNE – A
JULY – B
AUGUST – C
SEPTEMBER – D
PERCENT FREQUENCY OF OCCURRENCE
FORK LENGTH (mm)
60-69
70-79
80-89
90-99
100-109
110-119

Cladocerans were consumed by proportionately more perch in length groups up to 99 mm than by larger fish in the June sample (Fig. 17-A). They declined both in frequency of occurrence and in relative bulk of the diet for larger perch. The two species of amphipods were consumed by perch over the entire size range examined. Hyalella were eaten by perch less than 90 mm long while Gammarus were eaten more frequently than Hyalella by perch greater than 99 mm in length and comprised the greatest bulk of the diet of perch longer than 109 mm in length. Immature aquatic insects were eaten by all sizes of perch with no general trends evident. Perch were eaten relatively infrequently by perch of all sizes but constituted the bulk of the diet for perch from 100-109 mm in length. The percentages of perch with empty stomachs remained relatively constant over all length intervals.

Of the two species of amphipods consumed by perch during the July netting, Gammarus were eaten by proportionately more and Hyalella by fewer perch as length increased (Fig. 17-B). Their respective contributions to the total weight of the stomach content changed accordingly. Fish and immature aquatic insects were eaten by perch over the entire length range examined with no definite trends evident. Further, no apparent differences were observed in the percentages of perch in the various length intervals having empty stomachs.

During the August netting period (Fig. 17-C), amphipods were found to decrease in their relative occurrence with increasing length of perch while their contribution to the bulk

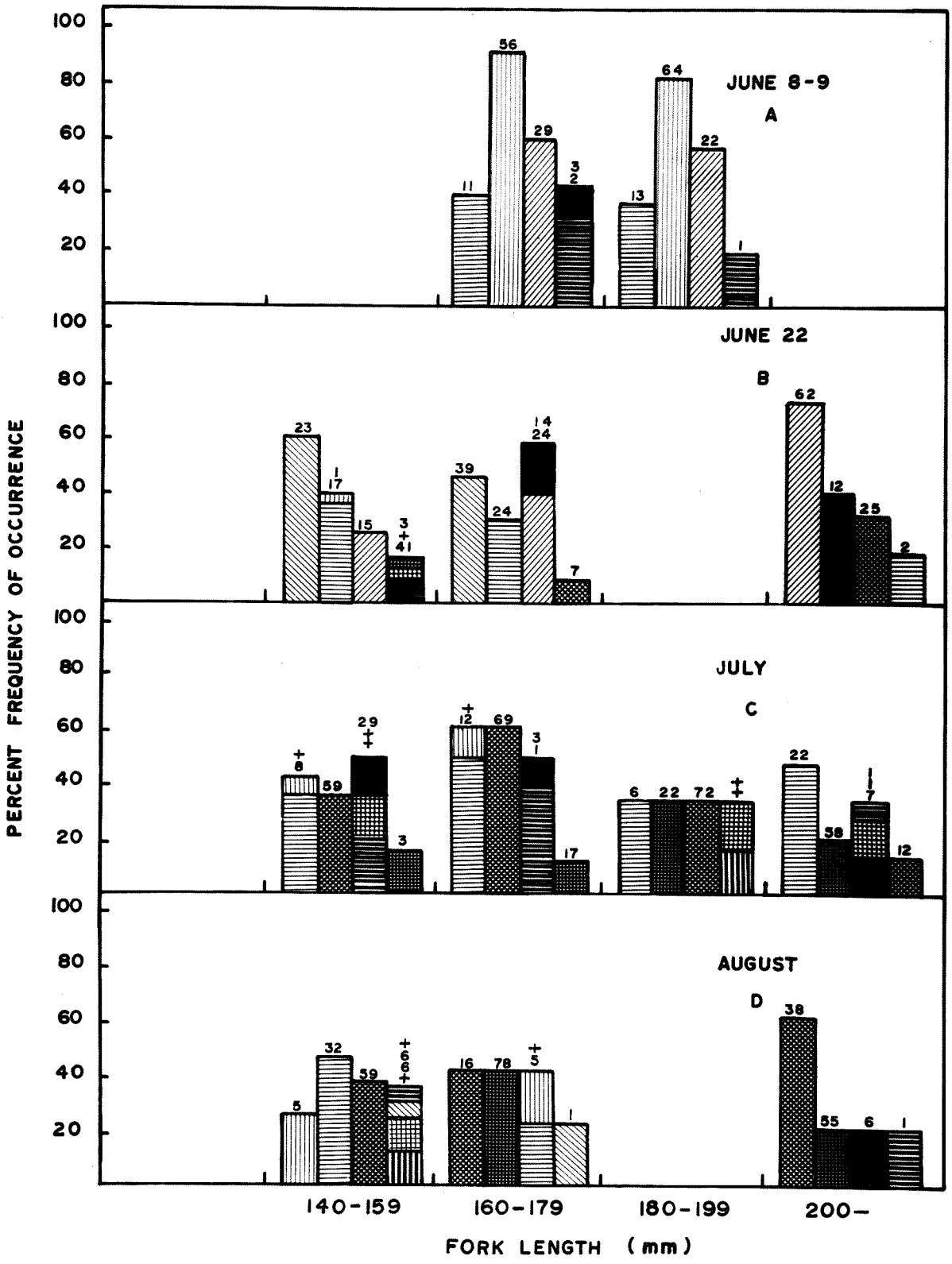
of the diet remained relatively constant. Fish were eaten by proportionately more perch as length increased but their percentage by weight decreased. Crayfish and immature aquatic insects occurred infrequently and did not show any length related trends. The percentage of perch with empty stomachs remained relatively constant over the lengths examined.

Cladocerans were consumed in the September sample (Fig. 17-D) by most perch in each length group and constituted the greatest bulk of the diet, but their contribution decreased in perch greater than 99 mm long. Immature aquatic insects, fish amd amphipods were eaten by perch less than 100 mm. Crayfish were consumed by perch longer than 90 mm and constituted the bulk of the diet in perch 109 mm and more in length. Among perch less than 80 mm long 2% of the stomachs were empty while in perch longer than 89 mm 42% of the stomachs were empty.

The percentage occurrence and weight of major food items eaten by adult perch during 1969, grouped into two cm length intervals for those in which sufficient numbers of perch were sampled are shown in Fig. 18. No apparent differences were found in the occurrence and weight of food items eaten on June 8-9 by perch between the two length intervals analysed (Fig. 18-A). The percentage of perch with empty stomachs was 9 for perch from 160-179 mm and 33 for perch from 188-199 mm.

In the June catch amphipods and cladocerans were eaten by proportionately fewer perch as their length increased (Fig. 18-B). Hyalella were only eaten by perch below 159 mm

Fig. 18 Changes in the percentage occurrence of major food items with size of adult perch collected during 1969 diurnal netting experiments. Numbers above rectangle indicate the percentages by weight.


JUNE 8-9
A
JUNE 22
B
JULY
C
AUGUST
D
PERCENT FREQUENCY OF OCCURRENCE
100
80
60
40
20
140-159
160-179
180-199
200-
FORK LENGTH (mm)

while cladocerans were only eaten by perch below 179 mm. Increasing proportions of immature dipterans, dragonfly nymphs and fish were eaten as perch length increased. Dipterans increased in relative weight in the diet with increasing perch size and comprised the major portion of the diet in fish over 199 mm in length. In contrast, dragonfly nymphs comprised the bulk of the diet for perch from 140 and 159 mm in length. The percentage of perch with empty stomachs remained relatively constant among length intervals.

In July, Gammarus were consumed by approximately equal percentages of perch of all lengths but only constituted an important part of the diet of perch greater than 199 mm in length (Fig. 18-C). Hyalella were only eaten by perch less than 179 mm in length. Immature aquatic insects were eaten by perch over the entire range of lengths investigated and, with the exception of dragonfly nymphs in perch from 140 to 159 mm long, did not constitute an important portion of the diet by weight. Fish were consumed by proportionately more perch from 140 to 159 mm long and comprised the greatest bulk of the diet in fish from 140 to 179 mm in length. Crayfish were taken as food by a larger percentage of perch over 179 mm long. In these larger perch they constituted the largest contribution to the diet by weight. The percentage of perch with empty stomachs was greatest in fish over 199 mm in length.

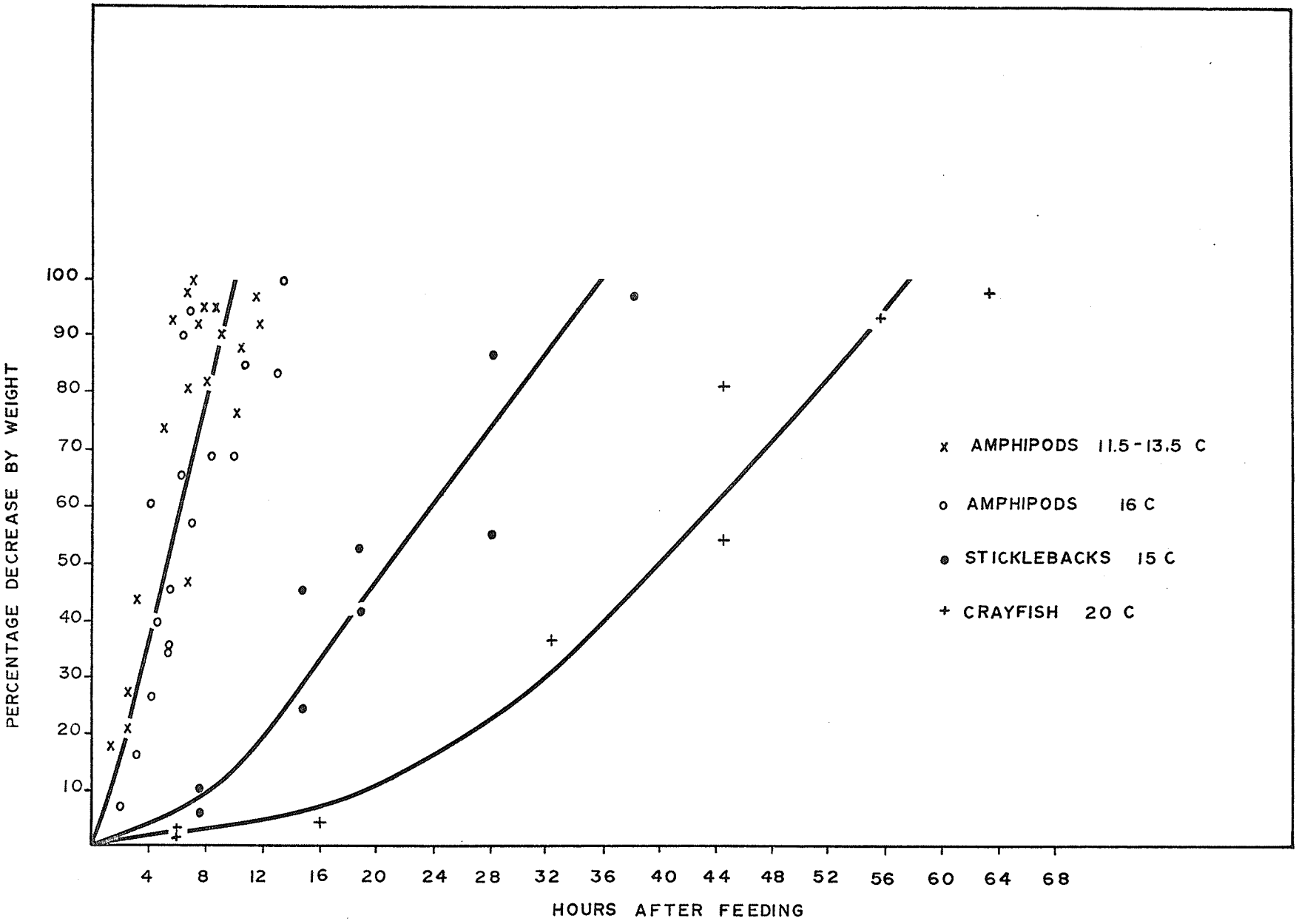
Cladocerans constituted a minor portion of the diet by weight (Fig. 18-D) and were only eaten by perch less than 180 mm in length. Amphipods were eaten by proportionately fewer perch

as length increased and were not present in the stomachs of perch greater than 179 mm long. Immature aquatic insects occurred infrequently in perch stomachs over the size range investigated and only dragonfly nymphs comprised an important portion of the diet of perch longer than 199 mm. Fish were taken as food by perch in all length intervals and comprised the greatest bulk of the diet by weight for perch ranging in length from 140 to 159 mm. Crayfish were consumed by greater numbers of perch and comprised the greatest proportion of the diet by weight for perch longer than 160 mm. The percentage of perch with empty stomach decreased with increasing length.

Gastric Digestion Rates

Curves indicating rates of gastric digestion in adult perch were fitted by eye to the data from two experiments using amphipods as food and from single experiments using sticklebacks and crayfish as food (Fig. 19). Variation among individual perch was great. This is especially evident in the results of the experiments using amphipods as food where the variation increased with time. A single curve was fitted to the data from the amphipods experiments because values obtained from the two experiments were similar. The degree of digestion increased as an apparent linear function with increasing time of residence in the stomach. Digestion of the softer ventral parts commenced almost immediately. After four hours, digestion of these ventral parts was extensive, with loss of exoskeleton plates and appendages but the animals

Fig. 19 Digestion rate curves from experiments conducted on adult perch during 1969 and 1970.


PERCENTAGE DECREASE BY WEIGHT
100
90
80
70
60
50
40
30
20
10
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
64
68
HOURS AFTER FEEDING
x AMPHIPODS 11.5-13.5 C
o AMPHIPODS 16 C
STICKLEBACKS 15 C
+ CRAYFISH 20 C

retained their general body form. After seven hours bodies were fragmented but still recognizable. After nine hours the stomach contents were composed of a mulch of exoskeleton and fluid. Passage into the intestine commenced between three and five hours after ingestion. At first, whole individuals were passed into the intestine but, during later stages of gastric digestion fragments were passed into the intestine. Average time to 50 and 95% digestion were estimated to be 5.5 and 10.5 hrs respectively.

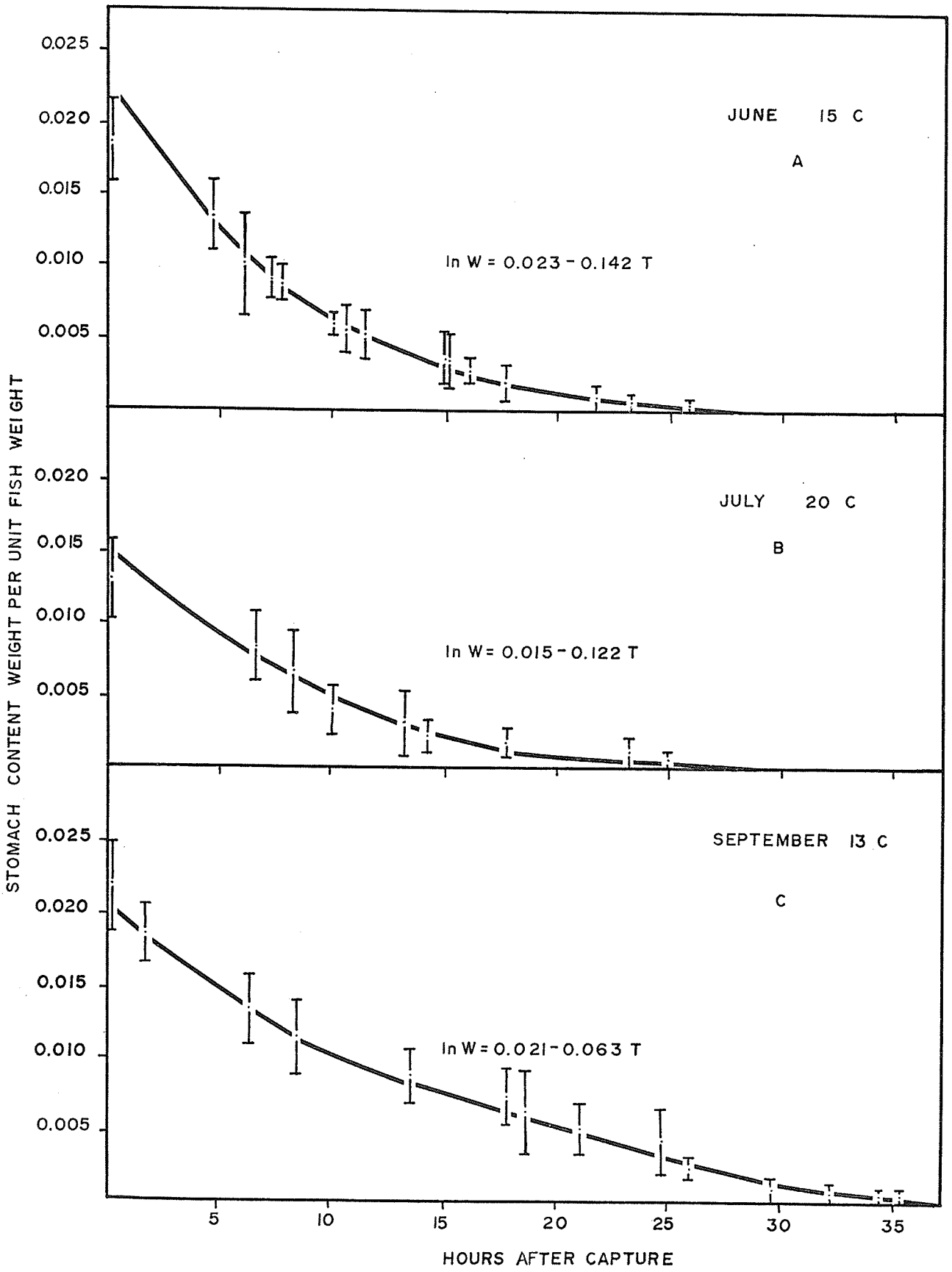
The percentage digestion of sticklebacks tended to increase in a curvilinear manner with time after an eight hour lag delay period (Fig. 19). After eight hours, skins were partially removed and internal organs exposed. After 15 hrs the skin had disappeared the head and musculature of sticklebacks were considerably digested. Passage into the intestine was noted after 19 hrs. After 28 hrs the flesh was separated from the backbone and the state of digestion was advanced. After 38 hrs a mulch of skeletal structures and fluid remained. Average times to 50 and 95% digestion were estimated to be 20.5 and 36.0 hrs respectively.

Similarly, the percentage digestion of crayfish with time tended to be linear after a lag phase (Fig. 19). The lag phase was more pronounced than for sticklebacks but the period of rapid digestion was parallel. Of the twelve adult perch fed crayfish, four regurgitated; therefore, data from these fish were disregarded. Regurgitation apparently occurred at various times since partially digested remains were found in

two cases. After six hrs digestion was slight. Only appendages and antennae were lost. After 16 hrs the exoskeleton was soft and the abdomen partly digested. Further softening and digestion of the ventral surface was evident after 32 hrs. After 44 hrs the body of the crayfish was fragmented and digestion of all parts was extensive. Passage into the intestine was noted at this time. Further fragmentation and digestion was observed after 55 hrs with passage of appendages into the intestine. After 64 hrs the stomach contents constituted a mulch of exoskeleton and fluid with the presence of a large portion of a crayfish abdomen in the perch intestine. Approximate times to 50 and 95% digestion were estimated to be 36.0 and 56.0 hrs respectively.

Stomach content depletion curves, fitted by eye, for juvenile perch (Fig. 20) indicated that the relationship between stomach content weight per unit fish weight with time was curvilinear in all three experiments. Variation was initially great since perch utilized in these experiments had various amounts of food in their stomachs as a result of different levels of feeding activity prior to capture and different food items. This variation, however, decreased with time and became very small as perch stomachs became empty. After data were converted to natural logarithms it was found that near the end an experiment points deviated from a straight line as the number of empty stomachs increased. These data were not included in analyses. Instantaneous rates of depletion were -0.142 ($\pm$ 0.010), -0.122 ($\pm$ 0.015) and -0.064 ($\pm$ 0.006) respectively

Fig. 20 Digestion rate curves from experiments conducted on juvenile perch during 1970.


JUNE 15 C
A
ln W = 0.023 - 0.142 T
JULY 20 C
B
ln W = 0.015 - 0.122 T
SEPTEMBER 13 C
C
ln W = 0.021 - 0.063 T
0.025
0.020
0.015
0.010
0.005
5
10
15
20
25
30
35
STOMACH CONTENT WEIGHT PER UNIT FISH WEIGHT
HOURS AFTER CAPTURE

from the three experiments. Calculated times to 50 and 95% digestion, for a constant intercept were found to be 5 and 32 hrs for the June experiment, 6 and 38 hrs for the July experiment and 11 and 72 hrs respectively for the September experiment.

The results of an analysis of covariance, designed to test the hypothesis that there were no significant differences in slopes between experimental lines indicated that no significant differences existed between the slopes of the June and July experiments ($F = 2.149$; $P > 0.05$) but the slope calculated from the September experimental data was significantly different from both June and July (respectively: $F = 148.240$, 19.320; $P < 0.05$). Both the temperatures and components of the diet differed in each experiment and may be considered major factors governing the digestion rate in each experiment. In the June experiment, conducted at 15C, cladocerans comprised 32%, amphipods 34%, insects 17% and fish 12% of the total stomach content weight. Amphipods comprised 69%, fish 29% and crayfish 7% by weight in the July experiment conducted at (13 C), cladocerans constituted 69%, amphipods 12%, crayfish 11% and fish 1% of the total diet by weight. Fish size did not vary greatly between experiments and is probably not a major factor modifying digestion rate in these experiments.

Daily Food Consumption

Calculated values of average daily food consumption of both the individual food species and the total of all species

by juvenile perch are shown in Table 6. Since the daily intake of each component of the diet was determined from their

Table 6. Estimated average daily consumption by juvenile perch for both individual and total food organisms expressed in units of wet weight per unit of fish weight.

	Average daily consumption			
Food Organisms	June	July	August	September
Cladocera	0.00888	-	-	0.02741
Gammarus	0.00662	0.00796	0.00261	0.00304
Hyalella	0.00304	0.01599	0.00643	0.00133
Crayfish	-	0.00020	0.00224	0.00387
Diptera	0.00304	0.00006	0.00006	0.00010
Other Insects	0.00282	0.00017	0.00089	-
Perch	0.00071	0.01040	0.00923	-
Sticklebacks	0.00209	-	0.00933	0.00046
$\sum$	0.02743	0.3478	0.03079	0.03621
Total % of body weight	2.74	3.48	3.08	3.62

relative percentage by weight in the diet, food items with a slow rate of digestion were overestimated while those with a fast rate of digestion were underestimated. However, the relative differences are evident. In June, the average daily consumption was 2.74% of body weight per day with cladocerans and amphipods comprising the bulk of the food intake. Values were 3.48 and 3.08% per day for July and August when fish and amphipods comprised the greatest bulk of the diet. In September, when the diet was largely composed of cladocerans,

the average daily consumption was 3.62% of body weight per day.

Comparisons between calorific intake per day calculated from the calorific equivalents of the various food items and possible levels of metabolic expenditure (cal/day) are shown in Table 7. These results suggest that the daily metabolic

Table 7. Comparisons of calculated calorific intake to possible levels of metabolic expenditure for juvenile perch.

Month	Mean Fish Wt.(g)	Daily Intake (g)	Daily Intake (Cal./day)	Temp.[1] (C)	Metabolic Expenditure (cal./day)[2] $\alpha = 0.30$	$\alpha = 0.181$
June	5.6	0.1536	140.7	17.0	213.3	127.6
				8.7	91.3	55.0
July	5.9	0.2352	181.7	21.1	271.2	191.3
				11.0	121.2	72.8
August	8.9	0.2740	234.7	18.2	268.5	203.8
				11.2	172.0	101.2
September	5.1	0.1847	165.1	13.0	134.0	74.3
				9.5	94.2	57.9

1. The upper figure for each date represents surface temperature whereas the lower is the mean 0 - 20 m temperature.

2. Values were obtained using two values of α.

expenditure, which was assumed to be twice the resting metabolism, was greater than the calorific intake for surface temperatures but less for the average water temperature using Winberg's (1956) ideal level of metabolism ($\alpha = 0.30$ ml O_2/g/hr) for June, July and August. The calorific intake approximated

metabolic expenditure for June, July and August using surface temperatures and Winberg's (1956) level of metabolism for yellow perch (α = 0.181 ml O_2/g/hr). However, in September the calorific intake was greater than metabolic expenditure in all cases. In all comparisons using both levels of metabolism and average water temperature the calorific intake per day was greater than the metabolic expenditure using the average water temperature.

DISCUSSION

Sampling Problems

Many assumptions concerning sampling could not be met in this study because perch were not randomly distributed. Furthermore, distribution was variable according to season and fish size. Choice of sampling locations, although initially selected for similarities in depth and aquatic vegetation, depended largely on the local abundance of perch. A bias for perch feeding in the areas sampled may have occurred but cannot be considered great since comparisons between areas (Fig. 15-B and C) showed minor differences among areas in the major food items eaten. The relatively low numbers of perch caught in deep water and the steep-sided nature of most of the basins (Fig. 1) suggests that feeding by the population was negligible outside the sampling areas. It is conceivable, however, that abundance, availability and diversity of forage species varied among regions of West Blue Lake depending upon differences in depth, substrate and vegetation. Differences in food habits with respect to depth (Fig. 15-D) may not be considered as a source of error for seasonal comparisons since at all times nets covered a wide range in depth. Day to day variations in the kinds and amounts of food eaten by perch were not great. This was evident from samples caught in successive days at the same location. Both the average degree of stomach fulness and

the kinds of food items eaten compared favourably. The use of gill nets, in this study, resulted in perch being selected by size depending on the mesh size used. Since food eaten by perch were found to vary with respect to fish size, the food consumed of perch collected by a particular mesh size can only be regarded as representative of that segment of the population sampled. Also capture rates of perch by gill nets depended on activity of individual fish and their local abundance, plus presence of other fish species. In addition, the avoidance of gill nets during the day was probably great since nets were readily visible in shallow water.

Despite limitations imposed on this study by problems in sampling, the methods employed were those best suited to the lake and the basic problems of this study. Also these difficulties are inherent in most studies of this nature but tend to be ignored or considered of minor importance. (Keast and Welsh, 1968; McCormack, 1970).

Diurnal Feeding Habits

From results of diurnal netting experiments it was not evident that perch fed at night. Examination of stomachs in the early morning revealed that the percentage of perch with empty stomachs was generally high. Those with food generally contained items either consumed in the previous day or that were just recently consumed.

Changes in both the quality and quantity of food items

eaten by yellow perch were found to vary over the day. For two reasons, no attempt was made to test for differences in the kinds of food items present in the stomachs of perch from the various time periods within diurnal nettings. First, food items which were only consumed during one time period were still present in the stomachs in successive periods. Second, Hanson and Graybill (1956) showed that as sample size increases, diversity of food items consumed increases. Thus, the variability of the results increases with sample size until this variability stabilizes at an adequate sample size. Since sample sizes were largely limited by activity or abundance of perch over the day, limitations may be imposed on interpretation of the data. Inadequate sample sizes may obscure differences which might occur between successive samples or may lead to wrong conclusions. In this study an attempt to increase sample size was made by grouping fish within the diurnal netting experiments. Despite limitations the results of juvenile perch diurnal netting experiments may be accepted as representative of feeding in nature since sample sizes were gradually large and variations in diet was small. However, with adult perch results should be treated with suspicion since the diet was variable (both in size and species composition. Some food items were eaten previous to the netting period and the sample sizes were generally smaller than those for juvenile perch.

It became apparent that food items in some months tended to be eaten by perch at certain times of the day while others

occurred in perch stomachs throughout the day. Also, from examination of the stages of digestion it was possible to determine if items were recently digested or not. Two contributing factors to changes of food items eaten by perch over the day are diurnal differences in the distribution of perch and changes in the availability of their food organisms. Schools of perch in Lake Mendota have been observed to undergo pronounced onshore movements during the summer months at well-defined feeding areas before sunset and to a lesser extent after sunrise (Hasler and Bardach, 1949). Hasler and Villemonte (1953) showed that schools of perch broke up at sunset and settled to the bottom where they remained motionless. At sunrise perch rose from the bottom and moved out into deeper water. In this study, although there was evidence for diurnal migration and nocturnal inactivity (Fig. 4) the timing and nature of perch movements could not be determined. Assuming that this migration takes place in West Blue Lake food items present in perch stomachs at various times of the day may reflect regions inhabited by perch prior to capture. For simplicity food items eaten by perch were placed into two categories. One category included cladocerans and Chaoborus sp. which may be assumed to be eaten in open water, and another included benthic insects, amphipods, crayfish and fish which may be assumed to be eaten in littoral regions. These categories are arbitrary and are subject to differences in food habits over the season. When one or the other of these categories

predominated in the diet, little change in food habits over the day was observed but when a mixture of the two occurred a change was evident. In the first category, when Chaoborus sp. occurred in the diet (Fig. 9-A and B) they were found most frequently and in a freshly ingested condition in the morning when they constituted a large percentage of the diet by weight. Teraguchi and Northcote (1966) have shown that Chaoborus sp. larvae undergo diel vertical migrations being nearer the surface at night. LaRow (1968) found that pupae of this genus emerge at night. When cladocerans occurred in the diet (Fig. 7-A and D) they were only eaten in the morning and evening but the duration over which they were eaten extended further into the morning and commenced earlier in the evening. Bell and Ward (1971) demonstrated that D. pulex, in West Blue Lake, undergo a typical diel vertical migration being nearer the surface at night. Therefore, the greater occurrence of food items in the first category in the diet is presumably a result of interactions of predator and prey at certain times of the day when their distributions overlap.

Amphipods will be discussed as representatives of the second category since previous work has been done on them in West Blue Lake. Briefly, amphipods were present in perch stomachs throughout the day with larger numbers occurring in the morning and evening periods. Biette (unpub.) found H. azteca and G. lacustris to be most numerous in the shallow regions of the lake where rooted aquatic vegetation existed.

Neither species was found in great abundance below 4 m and did not show diel variations in abundance and distribution. However, from personal observations and the results of Mundie (1959) suggest that a diel variation of abundance and distribution may occur but this may be a seasonal event. Benthic aquatic insects, crayfish and fish were eaten by few perch and the stages of digestion were too variable to ascertain the time of feeding on them but it may be safely assumed that they were eaten on or near the littoral regions (Eggleton, 1952; Buschemi, 1961).

Diurnal changes in the degree of stomach fulness were generally bimodal with peaks occurring in the morning and evening. Peaks of stomach fulness for adult perch caught during the summer of 1969 (Fig. 8) may not necessarily indicate time of feeding since they were often caused by large food items, and as judged by their state of digestion, were consumed at some time prior to the netting experiment. Also, the results of the Kruskal-Wallis rank sum test did not show significant differences among time periods for these netting experiments. However, with adult perch caught during the spring of 1969 (Fig. 8-A) and juvenile perch caught during 1970 (Fig. 5) peak periods of stomach fulness may be regarded as periods of increased feeding activity. Evidence supporting this hypothesis was the high degree of variation in the amount of food present in the stomach prior and during these periods, the freshly ingested condition of the food items, and the low percentage of empty stomachs. Fur-

ther diurnal changes in average number of small food items in perch stomach corresponded well with peak periods of stomach fulness (Fig. 7 and 10). The unimodal character of the feeding pattern for juvenile perch caught during August (Fig. 5-C) differs greatly from the other patterns. Sampling error may be the cause of this but since perch were collected over a three day period other factors may be the cause. It is conceivable that a difference in availability and distribution of food items may have caused a large portion of feeding to occur in the evening when food may be more easily captured. In contrast, feeding may have been continuous over the day reaching a maximum in the evening. Timing of the peak periods of stomach fulness was variable for juvenile perch and could not be attributed to differences in sunrise and sunset over the season and did not correspond to peak catch rates of perch. It is probable that with increasing or decreasing light intensity food items became more available as they follow an optimum light intensity and at lower light intensities may be more vulnerable to predation. It is probable that light intensity is the prime factor triggering feeding but the general lack of agreement of feeding activity with the timing of sunrise and sunset suggests that other mechanisms may be involved. Explanations for these differences are probably associated with the behaviour and distribution of the food items eaten during each netting experiment and the depth from which perch migrate to reach the feeding grounds. Bardach (1955)

recognized a diurnal migration for perch and showed that the magnitude of migration depended upon depth of thermocline.

The results of this study are in general agreement with the little evidence in the literature pertaining to diurnal food habits of yellow perch. Hasler and Bardach (1949) showed that perch fed while moving parallel to shore and that Daphnia sp were eaten in the greatest quantities before sunset. Scott (1955) reported that perch (135 mm), while feeding on cladocerans, had two peaks of stomach volume with the greatest occurring in the evening. Keast and Welsh (1968) described perch (90-130 mm) to have two peaks of stomach fulness with the highest peak in the evening. Unlike the results mentioned here, they found the species composition of the diet to be similar in both periods.

Temporal Feeding Habits

Changes in the diet composition of adult and juvenile perch over the sampling periods were great as demonstrated by the significant results from chi-square analyses (Table 3 and 4). The large proportion of aquatic insects taken by perch in the spring (Fig. 12 and 14) was primarily the result of emerging Chaoborus sp. pupae which were virtually absent from the diet in late summer. Eggleton (1952) showed that aquatic insect emergences usually take place in the spring causing temporary fluctuations in diversity of available food resources. The general decrease of other aquatic

insects in the diet over the season may have been a result of a decrease in their availability or abundance. Ball and Hayne (1952), Gerking (1962) and Anderson and Hooper (1956) have shown that the numbers and volume of benthic insects is lowest during mid-summer. Emergences, natural mortality, fish predation and the fact that the biomass was largely composed of immature instars were shown to be causal factors.

Seasonal changes in the proportion of perch feeding on amphipods and their relative importance by weight may be explained by changes in the abundance and size structure of amphipods, their availability and alternate food sources. Biette (unpub.) investigated seasonal differences in abundance and size structure of H. azteca and G. lacustris in West Blue Lake. He found that abundance of both species was greatest during June and July when immature individuals composed the greatest percentage of the population. The number of amphipods decreased over the summer and winter. They formed the basic food item for adult perch throughout the sampling period of 1969. H. azteca comprised the bulk of the diet in the spring (Fig. 14-A and B) which may be a result of their greater abundance in shallow regions during spawning activities and their increased availability due to the absence of protective vegetation. Despite the fact that amphipods were eaten by the majority of adult perch over the summer the smaller individual size of amphipods and the presence of larger food items may have caused the percentage by weight of amphipods to decline. Amphipods

were only taken by the majority of juvenile perch in July and August of 1970 (Fig. 12-B and C). The possible increased availability and abundance of alternate food sources such as Chaoborus sp pupae and cladocerans may have caused predation on amphipods during June and September to be low (Fig. 12-A and B). In contrast, decreased abundance of amphipods in September may have caused perch to turn to an alternate food source.

The absence of cladocerans from the diet in certain months of both adult and juvenile perch is of interest to this study. Seasonal changes in the abundance of cladocerans in West Blue Lake have been determined for 1969 and 1970. In 1969 cladocerans, collected by a 16 l Van Doren bottle, occurred in the greatest numbers in June and July. In 1970, data which were supplemented by vertical net hauls showed cladocerans to occur in greatest numbers in late spring and September. It was first thought that increased abundance of cladocerans during different times of the season may explain the results. This seems to be the case for their occurrence in the diet for adult perch in early summer and for juvenile perch in June and September. However, the occurrence of cladocerans in the diet of adult perch during August, when their abundance was relatively low may be explained only by these perch foraging in deeper water. Another explanation may be that perch are completely isolated from cladocerans during certain months by differences in vertical distribution.

Increased predation on fish and crayfish during summer by both adult and juvenile perch may indicate scarcity and/or lack of availability in their basic food items. Both sticklebacks and crayfish were abundant throughout the sampling periods; therefore the increased predation of them cannot be explained on the basis of increased numbers. It is probable that they serve as alternate foods taken in only when the basic foods of perch reach low levels.

Another factor which may cause a shift in diet over the season is the diversity of the rooted aquatic vegetation. Lundbeck (1927) demonstrated that the abundance and diversity of benthic animals was greatest in regions of aquatic vegetation. The seasonal succession of this aquatic vegetation may cause certain food items to become unavailable to perch by affording cover.

The significant correlation between the percentages of empty stomachs and water temperature was not solely caused by increased digestion rate at higher temperatures in turn causing a high frequency of perch with empty stomachs in the catch. Two other factors influencing this trend were the abundance and kinds of forage animals. With a decreased abundance of food, which may have occurred in late summer, perch may have required more time to search for food. Also, the shift in the diet to larger food items (fish and crayfish) in late summer may have required more time for search and capture than with smaller food items. The increase in frequency of empty stomachs with water

temperature may then be thought to be a function of increased digestion rate, food abundance and food size. McCormack (1970) noted a large proportion of perch in Windermere to have empty stomachs in August. She did not attempt to explain the results but suggested that blue-green algae may act to suppress feeding. This may have been the case in West Blue Lake but it is doubtful since perch may forage in deeper water to avoid toxic metabolites.

Changes in stomach content weight per gram of fish weight for adult and juvenile perch during the sampling periods were not great and significant differences were probably caused by empty stomachs. The lack of correlation of stomach fulness with day length and water temperature suggests that these variables do not influence the seasonal changes in average stomach fulness. Differences between months may be a result of feeding activity or abundance and kinds of the food items. The result in Fig. 11 suggested that feeding activity was high in early June after spawning and in September when development of gonads in sexually mature fish was evident. Decreased food abundance may be the cause of low values for adult and juvenile perch in August. Despite differences in the percentage of perch with empty stomachs and changes in their diet during the sampling periods, mean stomach fulness remained relatively constant. Apparently, the population maintains a relatively constant level of stomach fulness and the presence of a large percentage of perch with empty stomachs is opposed

by perch feeding on large food items. Other studies also have shown that perch change their food habits during the year and that the changes are a function of the differences in distribution, abundance and diversity of the forage species (Pearse and Achtenburg, 1920; Moffet and Hunt, 1945; Maloney and Johnson, 1957 and McCormack, 1970).

Feeding with Size of Perch

Changes in size of food organisms and composition of the diet with increasing size of yellow perch have been reported (Nurnberger, 1930; Allen, 1935; Tharratt, 1959 and Antosiak, 1963). The prime factor governing the size of food items consumed is mouth size. For a given size of perch mouth gape limits the maximum size of the food items which may be eaten. Another factor determining the relation between fish size and food size is energetics. The amount of food required by a fish increases with size, therefore an increased number of food units will be needed if food size is constant. Consequently growth will be limited by the problem of obtaining sufficient numbers of the food item. If this is to be avoided, the fish must take larger food units either by consuming larger sizes of a single species or by taking other larger foods.

My results are in general agreement with those of previous investigators; however, there were instances where no apparent differences or even reversals of the trend were evident. Other factors, besides those of mouth size and

energetics, must act to modify the relation between fish size and the composition of the diet. First, if over a limited size range of perch, the forage species were all of edible size and available in sufficient numbers so that all sizes of perch were able to feed to capacity no differences in the diet with respect to fish size would be evident. Second, since larger perch tended to inhabit deeper water than smaller perch differences in the available food supply may result in differences in feeding among sizes of perch. If small food items are abundant in deeper water (eg. Chaoborus sp) predation on them by larger perch may cause a reversal of the trend. Further, since perch form schools composed of multi-sized individuals and smaller perch often outnumber larger perch, they must be in continual intraspecific competition for food. Large perch may feed on larger food organisms as a direct result of their larger mouth size or may be forced to consume larger food items because small perch have cropped off the smaller sizes. In both cases the net result is to reduce intraspecific competition for food.

The decrease of cladocerans with increasing fish size, when present in the diet (Fig. 17-A and C), in both occurrence and bulk may be a function of energetics but the mere increase of mouth size resulting in alternate food sources to become available may explain the shift in diet. Further, gill rakers may become less efficient in straining out zooplankton as perch increase in size (Galbraith, 1967). The

size of individual food items in relation to fish size is believed to be of considerable importance in determining its occurrence and contribution to the bulk of the diet. When amphipods predominated in the diet the smaller species H. azteca decreased in occurrence with increasing size of perch while the larger species G. lacustris increased (Fig. 17 and 18). Also, both occurrence and individual size of fish and crayfish tended to increase with size of perch and in larger perch were responsible for the greatest bulk of the diet. With the exception of dragonfly nymphs which were mostly eaten by larger perch (Fig. 18) other aquatic insects tended to be eaten by all sizes of perch sampled.

Stomach content weight was found to increase with fish size but not in direct proportion to that of weight (Fig. 18). This suggests that as fish grow they are capable of consuming less in proportion to their weight. This comparison is based on the assumption that the average content weight is a constant fraction of the amount consumed. This depends largely upon the digestion rate for perch of different sizes being constant. However, as shown by the digestion rate experiments (Fig. 19), crayfish and sticklebacks had comparatively slow rates of digestion than amphipods. Since these large food items occurred more frequently in stomachs of larger perch the average rate of digestion may be seriously reduced. Also, Hunt (1960) and Pandian (1970)showed that older fish have slower rates of digestion than younger fish. The effect of both of these facts indicate that consumption

of food by older perch may be reduced further than the relationship between stomach content weight and fish weight indicated. The lack of direct proportionality in the above relationship has been explained by a decrease in stomach capacity relative to weight with increasing fish size by Ishiwata (1968-c).

The relationship between stomach content weight and fish size presented here may be biased by two factors. First, mean values of stomach content weight for any size range of fish may be an underestimate of an actual value since stomachs which were utilized may not be completely full or contained partially digested remains. However, the slope of the regression line may not be seriously affected if underestimates were constant over the size ranges investigated. Second, as stomach capacity increased, the range of the weight of the stomach contents increased (Fig. 16). This may have caused the average stomach content weight to be proportionately lower for larger perch.

The significance of the relationship between stomach content weight and fish size is that as fish grow they consume less, either as a result of a decrease in digestion rate or relative stomach capacity. This may be one of the main causes of the observed decrease in growth rate in older, larger fish which is observed in many studies. With further information concerning digestion rates of various food items by perch of different sizes and at various temperatures the above relationship may be used as a basis in determining

consumption rates for the population.

Rates of Gastric Digestion

Adult perch digestion rates for amphipods, sticklebacks and crayfish were determined at habitat temperatures approximating those occurring at the season when these animals predominated in the diet (Fig. 19). Differences in digestion rates may be explained largely on the basis of size of food items, their relative surface area and their anatomy. Amphipods were passed into the intestine whole and their relatively large surface area permitted rapid digestion. Sticklebacks and crayfish required extensive breakdown before passage into the intestine took place. Crayfish required more time to digest than sticklebacks because of their chitinized exoskeleton. This only affected the initial lag phase, after which the rates of passage into the intestine for crayfish and sticklebacks were similar. Regurgitation of crayfish may have been the result of stress from handling or force feeding. However, the occurrence of partial remains of crayfish in perch stomachs and intestines caught in the lake suggests that this may occur naturally, which complicates interpretation of their importance as a food source. Despite the temperature difference in the two amphipod experiments there was no apparent difference between the rates of digestion. This may have been a result of variations in digestion rate among individuals but a more feasible explanation was that the digestibility of individuals differed between the two experiments. Amphipods, used

in the first experiment may have been senescent since they were probably post-spawners (Biette, unpub.). This may have resulted in a relatively rapid digestion rate despite their larger size. In the second experiment the amphipods were small but intact. This difference in condition may have accounted for the similar digestion rates.

As with the adult perch digestion rate experiments, those for juvenile perch were also conducted at habitat temperatures (Fig. 20). The stomach contents of perch collected for the experiments were assumed to be representative of the food habits of the population segment sampled. Further the digestion rate curve was assumed to give an average rate for all food items. All three experiments showed an exponential decrease with time as described by Tyler (1970) suggesting that the rate of digestion at a given temperature and with similar food was dependent on the initial weight of the stomach contents. In theory such a relationship indicates that stomachs will never be completely empty. However, the effects of gastric juices and stomach motility is efficient in emptying the stomach. Differences in the rate of digestion between these experiments may be explained by the effects of temperature and the quality of food. The similar results of experiments in June and July, despite a 5 C difference in temperature, may be explained by the shift in diet from predominately cladocerans and amphipods in June to amphipods and fish in July. The combination of amphipods and fish in July may have acted to lower the rate of digestion and thus cause results of the

two experiments to be similar. Lower habitat temperatures in September is believed to be the reason for significantly lower rates of digestion than both June and July even though composition of diet was similar to June.

Difficulties arise in relating the results of both juvenile and adult experiments to perch digestion rates in nature because of variable results and the effect of experimental conditions. The considerable variation occurring among individuals may have been caused by different levels of metabolic activity and errors inherent in determining blotted dry weights of the food. Because of this variation and the small numbers of perch involved the estimated times to 50 and 95 percent digestion for adult perch were not precise. They are useful, however, in comparisons between experiments where definite differences were evident. In experiments conducted on juvenile perch individual variation was again great but may be attributed here to variation in amount of food ingested prior to capture. Results of these experiments give better estimates of the time to 50 and 95 percent digestion since sample size was larger and variation among individuals was reduced by determining mean values. Further difficulties in relating the results of perch digestion rate experiments to those in nature are the effect of handling stress, force feeding, and confinement, plus decreased activity resulting from confinement. All these factors affect metabolic rate and hence digestion rate. Daily and seasonal differences in kinds of food eaten, habitat

temperatures and activity further complicate the problem.

There is little information in the literature concerning the rates of gastric digestion for yellow perch. Pearse and Achtenburg (1920) determined digestion rate as time from ingestion to defecation, hence the results may not be comparable to those in the present study. However, they found this rate of digestion to increase with temperature and decrease for larger fish. The rate also varied with the type of food. Molnar and Tolg (1967) showed that the digestion rate for European yellow perch, with fish as food, increased with temperature from approximately 110 hrs at 5 C, to 50 hrs at 15 C and to 25 hrs at 25 C. The time of 36 hrs determined for sticklebacks from Fig. 19 is lower than the above values at 15 C. However, differences in experimental methods and conditions plus differences in fish and food size make comparisons difficult.

My estimates of digestion rates were determined as an intermediate step towards attempting to estimate daily food consumption. The significance of these experiments will become apparent subsequently, but the results of these few experiments indicate the need for future studies comparing the digestion and growth rates for fish which change their diet with season and mouth size.

Rates of Food Consumption

From knowledge of the diurnal feeding pattern (Fig. 5) and gastric digestion rates (Fig. 20) for juvenile perch

estimates of their daily consumption rates were determined. The validity of the method depended on several assumptions and possible inherent errors. The assumption that perch fed only during the day and exhibited a diurnal feeding pattern was met. Consequently stomach content data for fish captured during diurnal nettings and data from the digestion rate experiments were assumed to permit estimates of the average quantity of food present in stomachs for the segment of the population sampled. It was noted that variation associated with these mean values was great and, from the results of Bartlett's tests, was not homogeneous during the day. However, this variation was probably associated within day changes in feeding activity and not a result of sampling errors. An average value for a sufficiently large sample of fish was assumed since some perch may feed to excess during a day while others may not feed at all. Day to day variations in the daily meal are great and are dependent largely upon feeding during the previous days feeding (Moore, 1941; Magnuson, 1969 and Pandian, 1970). In these studies, data for individual fish were averaged for weekly intervals to obtain daily means. This procedure is similar to mine except that I assumed the behaviour of groups of fish was similar to individual fish during several days. The results of juvenile perch digestion rate experiments may be assumed to be valid estimates of rates in nature, but effects of stress and decreased activity may act to lower the rate, thus underestimating the daily consumption. The

assumption that the digestion rate curve was an estimate of the average rate of digestion for all food items was probably valid since stomach contents of perch used in these experiments contained all food items present in the diet at the time of the netting experiment. Since food items in stomachs of perch contained food items in various stages of digestion the average amount digested per two hour interval may be an underestimate of the actual amount; from the digestion rate experiments, only digested material was present in stomachs. This bias may not be great but could affect estimates at low levels of stomach fulness. Also, an underestimate may also have occurred with the amount digested, and hence the amount consumed, when perch feed to excess, forcing partially digested food into the intestine. Further, if average stomach fulness was not accurately determined for a given interval, the amount digested would also be incorrect. By successive under-and over-estimates throughout the day the net effect may cancel out error inherent in determining the degree of stomach fulness. Changes in composition of diet over the day was not sufficiently great to cause serious errors in determining daily food consumption.

Despite the above limitations, the method for calculating average daily consumption provided reasonable estimates based on comparisons of calorific intake to estimated levels of a daily metabolic expenditure (Table 7). These estimates are only rough approximations for obvious reasons but can be used to indicate whether my estimates of daily

consumptions were reasonable. The levels of metabolism are subject to variations with respect to environmental variables plus swimming and feeding activity, social facilitation, sex and state of maturity, parasitism and many other factors (Fry, 1957). Wohlschlag (1957) has noted that body weight and temperature accounted for most of the variability in oxygen consumption rates for fish and it should be noted that these variables were used in determining metabolic expenditures. Using surface temperatures to estimate metabolism the metabolic expenditures were greater than calorific intake for June, July and August (Table 7). This probably caused a serious overestimate and since perch may be found at a variety of depths being limited in their vertical distribution by the depth of the thermocline (Bardach, 1955) and average water temperature may be more appropriate. Results of these calculations showed that in all cases the level of metabolism was less than daily intake (Table 7). Since perch tend to remain in the region near and above the thermocline as well as venturing into deeper, colder water (Horak and Tanner, 1964) the level of metabolism using an average water temperature may be an underestimate. However, the levels of metabolism using surface and average water temperatures may represent extremes, since the estimated calorific intake fell between these values. No conclusions could be drawn from the estimates of metabolism using different levels of metabolism (α). For the purpose of this study

Winberg's (1956) ideal values (= 0.30) was used but this in itself may be subject to error. Another source of error which may affect the daily metabolic expenditure by fish in this study is the choice of two as a factor by which to multiply resting metabolism to obtain an estimate of metabolism in nature. Since perch exhibited a diurnal feeding and activity pattern, the factor of two may be an overestimate but again this is merely subjective. It is interesting to note when the greatest differences between calorific intake and metabolic expenditures occurred. Differences were greater in July and September than in June and August. In July, when water temperatures were the highest greater feeding activity may have resulted in a higher calorific intake. B. Wong (pers. comm.) showed that young-of-the-year perch in West Blue Lake had a greater specific growth rate in July than in any other month. In September, when water temperatures were lowest, growth was correspondingly reduced. However, high calorific intake may have been associated with development of gonads in fall prior to winter. The September sample was comprised of 80% males, of which all were sexually mature while the females had not yet reached sexual maturity.

Average daily consumption estimates for juvenile perch (Table 6) corresponded well with the average monthly stomach content weight (Fig. 12), suggesting that food consumption by perch in their natural environment is primarily determined by the quantity and quality of the available food organisms.

The effects of habitat temperature and daylength may be considered of secondary importance and may merely act to modify food consumption in different seasons. For example, when temperatures are high and when days are long food consumption may increase but if insufficient food is available the increase is nullified.

Rates of food consumption for adult perch were not determined because most of the assumptions underlying the method described in this study were not met, largely because of variability in the diurnal feeding pattern, from small sample sizes and diversity of the diet. In addition an average digestion rate could not be determined. However, generalizations concerning the seasonal changes in food consumption are possible. From results of food analysis and adult perch digestion rate experiments, it was apparent that the shift in diet from amphipods in spring to fish and crayfish in late summer caused daily consumption to decrease. For example, adult perch digest 3.6 and 5.6 meals of amphipods in the same time required to digest a meal of sticklebacks and crayfish respectively. Also, when perch fed on fish and crayfish, they did not commence feeding until the stomach was empty or when stomach contents were in an advanced state of digestion. In contrast, when perch fed on smaller food organisms (eg. amphipods) they continued feeding while passing food into the intestine. The net effect on both the frequency of feeding and the rate of digestion is that consumption of amphipods was greater than that of

fish or crayfish, hence a seasonal difference of food consumption which is again dependent upon the quality and quantity of the available food species. Significantly, adult perch which feed on fish and crayfish in late summer could not digest the meal by the next day, whereas juvenile perch had digested the stomach contents present in the evening by the next morning when feeding resumed. Components of the diet should be carefully considered when examining stomach contents from nettings in which fish and crayfish predominate in the diet. They may not constitute the most important part of the diet even though they constitute the bulk. Consumption of smaller food items may be greater and may not be truly represented by their apparent occurrence in stomachs because of their more rapid rate of digestion.

There is little information in the literature concerning the rates of food consumption for perch. Pearse and Achtenburg (1920) estimated the daily consumption of perch feeding on insect larvae to be seven percent by volume per day. The method employed was an indirect field procedure which may be considered an overestimate. Moore (1941), from laboratory experiments determined the daily consumption of perch to be approximately 3.5 percent of body weight per day which is comparable to the results obtained in this study (Table 6). Keast and Welsh (1968) determined the mean minimum ratio to be two percent of body weight per day which is an underestimate since the amount of food ingested over the day was not considered.

Relative Importance of Food Species

It is unlikely that there is any specific diet for perch. Food items of many kinds were eaten and it is probable that those which were eaten were most readily available. In nature the size composition, crowding, abundance and distribution of forage species varies from time to time and place to place. As a consequence of these constantly changing conditions, assessment of important food items is difficult. However, amphipods appear to be the most important food item since they occurred in a relatively large number of perch stomachs in all samples (Fig. 11 and 13) and were eaten by all sizes of perch; G. lacustris being important in large perch and H. azteca in small perch (Fig. 17 and 18). The importance by weight of amphipods in the diet may be obscured by their rapid digestion rate and presence of large food items. It is possible, however, that amphipods are not utilized as efficiently as other food items since amphipods tended to be egested in a partly digested condition; especially during heavy feeding. Cladocerans and immature dipterans may be considered as secondary in importance to amphipods since they only formed an appreciable segment of the diet at certain times of the year (Fig. 11 and 13). Cladocerans were only important sources of food for small perch while dipterans were taken as food by all sizes of perch. Again, their importance by weight may be underestimated by a rapid digestion rate, which probably approximates that of amphipods, and the influence of large

food items. Other insects appear to be of minor importance in the diet of all sizes of perch since they occurred in relatively few stomachs and comprised only a small fraction of the diet by weight. Although fish and crayfish constituted a large portion of the diet by weight they occurred in relatively few stomachs and were subject to strong seasonal variations. They may be considered as secondary to amphipods in these respects. Perch may utilize crayfish and fish more efficiently than amphipods because of their low rate of digestion and expend less energy in search and capture than with smaller food items. The large contribution of crayfish to the bulk of the diet may not be comparable to other food items directly because of the presence of a heavy exoskeleton of little food value. These factors further render the assessment of the importance of the various food items difficult. Fish appear to be taken as food by all sizes of perch while crayfish only constitute a large fraction of the diet by weight in adult perch (Fig. 17 and 18).

Trophic Position of Perch in West Blue Lake

Perch in West Blue Lake cannot be placed in one trophic level according to the trophic dynamic concept in aquatic ecosystems proposed by Lindemann (1942). Instead they occupy the third and fourth trophic levels and may be classified as secondary and tertiary consumers respectively. Perch in the third trophic level, consume food organisms that are

primary consumers including by weight cladocerans (9%), immature aquatic insects (22%), except predaceous dragonfly numphs and midge larvae (4%), plus amphipods (24%) and crayfish (11%). In the fourth trophic level the food of perch consists of fishes (32%) which are secondary consumers.

Larkin (1956) has noted the complexity and shortness of aquatic food chains. He ascribed the phenomena to be a function of the lack of specialization which in turn is afforded by a lack of opportunity in freshwater environments. He suggested that the ability of fishes to change their diet to take abundant foods and to compensate for absence of their usual diet by taking an alternate food is an important factor in regulating the abundance of fishes. This flexibility of diet is clearly evident in the present study and perch have been appropriately classified as a versatile feeder by Pearse and Achtenburg (1920).

Perch in West Blue Lake do not differ greatly in trophic position from those of other investigations. There is, however, some variability in the diet based on the regions of the lake from which the food is derived. In the present study benthic, plagic and nektonic organisms comprise approximately equal percentages of the diet by weight. Pearse and Achtenburg (1920), Ewers (1934) and Tharratt (1959) found insects to predominate in the diet of perch while Langford and Martin (1940) and McCormack (1970) showed that amphipods and plankton constituted the greatest bulk of the diet. Differences in endemic forage species, and lake morphology

make comparisons difficult. Further differences in food habits with respect to season and size of fish have been shown to be great and therefore may bias the results of this and other studies. It may be more appropriate to conclude that each population has its own food habits which are related to food preference and the relative abundance of different food organisms.

SUMMARY

Food habits of juvenile and adult perch in West Blue Lake, Manitoba were studied with respect to time of day, season and size of fish during the spring and summer of 1969 and 1970. Gastric digestion rates were determined using natural food items at habitat temperatures and in 1970 daily food consumption rates were estimated for juvenile perch.

1. Perch were captured in gill nets during the daylight hours only and were active feeders during mid-morning and early evening. Composition of food eaten varied over the day when the diet was composed of both pelagic and benthic organisms, whereas it remained relatively constant if the diet was primarily composed of littoral or pelagic organisms. Changes in the quantity and quality of food items eaten by perch over the day were explained by references to regions of the lake inhabited by perch and distribution and behaviour of the food supply.

2. Food habits of perch varied greatly over the seasons sampled. Items which formed basic constituents of the diet during one month may be absent during the next. Seasonal change in degree of stomach fulness was slight and differences could be partly explained by the occurrence of empty stomachs. Changes in diversity, abundance and availability of the food supply were presumably the main causes of both qualitative and quantitative differences in food habits.

3. Stomach content weight increased with weight of fish but not in direct proportion to that of weight. Therefore, as fish increase in size they consume less food probably being limited by their relative stomach capacity. As perch increase in size, there was a general tendency for perch to feed on larger sizes of a particular organism, or shift their diet to include other food organisms of a larger size.

4. Results from food analysis with respect to time of day, season and size of fish demonstrated variability in the diet of perch and inaccuracy of results which may be obtained from inadequate sampling for such a versatile feeder.

5. Gastric digestion rates, using adult perch at habitat temperatures, were largely a function of size and structure of the food items. Amphipods were digested faster than sticklebacks or crayfish, despite higher temperatures, since they were passed into the intestine in a partly digested condition. Sticklebacks and crayfish required more time for initial breakdown before passage into the intestine.

6. Gastric digestion rates, determined for juvenile perch at habitat temperatures using natural food items, were a function of both water temperature and the kinds of food items constituting their diet. A diet of fishes and amphipods yielded a digestion rate similar to a diet of cladocerans at a lower temperature.

7. A method was devised to estimate daily food consumption rates for juvenile perch based on knowledge of their diurnal feeding patterns and respective gastric digestion rates. Estimates of average daily consumption ranged from 2.7 to 3.6% of body weight per day and compared favourably to mean monthly degree of stomach fulness. Seasonal differences in the quantity and quality of available food supply were believed to be responsible for variation in daily consumption rates. According to calculated calorific intake and estimated metabolic expenditures, and excess of energy was ingested which may be channeled into growth.

8. Food consumption rates could not be determined for adult perch because of their failure to comply with basic assumptions. However, it was suggested that differences in the rate of digestion of a different food organism eaten over the sampling period may have led to decreased food consumption in late summer. It was further shown that food consumption was lower for adult perch than for juveniles.

9. Perch, in West Blue Lake, occupy the third and fourth trophic levels and may be classified as secondary and tertiary consumers deriving the greatest bulk of the diet from the former. Further, perch derive approximately equal percentages of their diet by weight from pelagic, benthic and nektonic organisms. Relative proportions of these food items in the diet of perch varied over the day,

seasons sampled and fish size making absolute generalizations difficult.

10. Amphipods formed the basic food items for perch in West Blue Lake since they were eaten throughout the sampling periods and by all sizes of perch. Cladocerans, immature dipterans, fishes and crayfish were of secondary importance since they showed variations with respect to sampling date and fish size. Insects, other than dipterans were of minor importance.

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APPENDIX A

Table A-1. Summary of dates, locations, weather conditions, temperatures, average daylengths and size ranges of yellow perch from 1969 and 1970 diurnal nettings.

Date	Location	Weather	Temp. (C) Surface	Temp. (C) $\bar{X}$(20m)	Day-length (Hrs.)	No. of Perch	$\bar{X}$ Fork Length (mm)	Range
June 8-9, 1969	4	Clear	12.5	8.2	15.0	40	184	163-209
June 22, 1969	3	Clear	14.5	11.0	16.0	87	170	127-264
July 23-24, 1969	3	Occ. Cloud	19.5	11.2	14.5	71	182	140-227
Aug. 24-25, 1969	5	Clear	20.5	9.5	13.0	51	166	143-220
June 23-24, 1970	3	Clear	17.0	10.3	15.25	99	81	53-119
July 21-22, 1970	1	Clear	21.1	10.7	14.50	124	82	67-117
Aug. 24-26, 1970	1	Occ. Cloud	18.2	13.0	13.0	66	94	75-114
Sept. 14-16, 1970	6	Occ. Cloud	13.0	13.2	11.50	86	78	66-110

APPENDIX B

Table B-1. Summary of stomach analysis and data from individual fish for the diurnal netting experiment conducted on June 8-9, 1969.

Fish Number	Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
24	1030	182	61	F	Hyalella		110	0.672
25	1030	209	107	F	Chaoborus	P	416	0.270
26	1030	179	67	F	Chaoborus	P	22	0.080
					Hyalella		57	0.252
27	1030	193	85	F	-		-	-
28	1030	185	68	F	Hyalella		40	0.179
					Ephemeroptera		1	0.017
29	1030	181	68	F	-		-	-
30	1030	168	58	F	Chaoborus	P	2	0.004
					Hyalella		47	0.200
31	1030	163	53	F	Gammarus		13	0.425
32	1030	203	64	F	Hyalella		28	0.103
					Hydracarinia		1	0.004
33	1030	176	79	F	Hyalella		27	0.215
					Gammarus		2	0.004
34	1030	182	59	F	Gammarus		3	0.122
					Hyalella		13	0.051
					Ephemeroptera		1	0.025
35	1030	175	64	M	Trichoptera		1	0.002
					Hyalella		19	0.065
36	1230	168	57	F	Tetragoneuria	N	1	0.154
					Hyalella		25	0.100
					Chaoborus	P	83	0.393
37	1230	171	64	M	Hyalella		202	1.113
38	1230	168	56	F	Chaoborus	P	226	0.767
39	1230	179	69	F	Gammarus		2	0.055
					Hyalella		22	0.100
40	1430	188	72	F	Hyalella		70	0.360
					Misc. insect		1	0.003
41	1430	177	64	F	Hyalella		4	0.096
					Gammarus		3	0.017
					Misc. insect		1	0.007
42	1430	184	75	F	Hyalella		104	0.653
					Chaoborus	P	59	0.305
12	1830	182	62	F	-		-	-
13	1830	197	82	F	Hyalella		33	0.171
14	1830	184	74	F	Hyalella		12	0.087
					Chaoborus	P	3	0.005
15	1830	177	66	F	-		-	-
16	1830	188	73	F	-		-	-
17	1830	203	99	F	Orconectes		1	0.159

Table B-1. Cont'd.

Fish Number	Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
18	1830	199	63	F	-		-	-
19	1830	195	84	F	Gammarus		1	0.020
					Hyalella		7	0.037
20	2030	182	64	F	-		-	-
21	2030	172	62	F	Hyalella		50	0.231
					Trichoptera		1	0.063
22	2030	186	69	F	Hyalella		36	0.251
					Gammarus		7	0.273
					Chaoborus	P	8	0.056
23	2230	192	74	F	Hyalella		23	0.033
					Chaoborus	P	12	0.037

L = Larvae, P = Pupae, N = Nymph, A = Adult.

Table B-2. Summary of stomach analysis and data from individual fish for the diurnal netting experiment conducted on June 22, 1969.

Fish Number	Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
126	0630	238	145	F	Tetragoneuria	N	1	0.106
127	0630	167	53	F	Chaoborus	P	21	0.107
128	0630	183	67	F	Chaoborus	P	31	0.110
					Chaoborus	L	4	0.005
129	0630	188	67	M	-		-	-
130	0630	190	85	F	-		-	-
131	0630	236	174	F	Tetragoneuria	A	3	0.062
					Chaoborus	P	304	0.604
					Chaoborus	L	4	0.002
132	0630	264	245	F	Chaoborus	P	324	2.000
133	0630	229	141	F	Chaoborus	P	41	0.206
					Tetragoneuria	N	2	0.887
134	0830	245	179	F	-		-	-
135	0830	159	42	F	Tetragoneuria	N	1	0.351
					Gammarus		1	0.021
					Chaoborus	P	1	0.004
136	0830	147	34	F	-		-	-
137	0830	163	52	F	Gammarus		2	0.308
					Chaoborus	P	1	0.003
					Daphnia		218	0.046
138	0830	150	39	F	Chaoborus	P	108	0.520
139	0830	160	48	F	Daphnia		542	0.214
140	0830	157	145	F	-		-	-
141	0830	251	174	F	Culaea		2	2.201
142	0830	259	189	F	Tetragoneuria	N	3	1.189
					Gammarus		9	0.326
					Chaoborus	P	1	0.004
143	0830	245	162	F	-		-	-
144	0830	238	156	F	Tetragoneuria	A	1	0.495
					Chaoborus	P	152	0.819
					Chaoborus	L	14	0.032
145	1030	220	140	F	Chaoborus	P	2024	10.185
					Chaoborus	L	64	0.392
146	1030	176	62	F	Gammarus		1	0.038
147	1030	148	57	F	Daphnia		70	0.027
148	1030	157	42	F	Daphnia		320	0.124
149	1030	144	33	F	Daphnia		151	0.068
150	1030	167	53	M	Chaoborus	P	22	0.049
151	1030	149	34	F	Gammarus		1	0.015
					Chaoborus	P	3	0.005
					Daphnia		350	0.118
152	1030	138	32	F	Daphnia		232	0.076
153	1030	161	44	F	Gammarus		5	0.122
154	1030	153	36	F	Gammarus		1	0.044
					Chaoborus	P	2	0.003

Table B-2. Cont'd.

Fish Number	Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
					Daphnia		164	0.060
155	1030	151	44	F	Gammarus		1	0.019
156	1030	159	40	F	-		-	-
157	1230	151	41	F	-		-	-
158	1430	194	88	F	-		-	-
159	1430	151	35	F	Hyalella		19	0.051
					Gammarus		5	0.091
160	1430	192	86	F	-		-	-
161	1430	157	39	F	Daphnia		51	0.014
162	1430	152	36	F	Gammarus		1	0.051
163	1430	169	56	F	Chaoborus	P	46	0.215
164	1430	178	70	F	Chaoborus	P	74	0.304
165	1430	158	46	F	-		-	-
166	1430	142	31	F	-		-	-
167	1430	146	34	F	Gammarus		6	0.201
168	1430	161	47	F	-		-	-
169	1630	159	46	F	Chaoborus	P	1	0.001
					Daphnia		10	0.003
170	1630	166	49	F	Gammarus		9	0.205
					Tetragoneuria	N	1	0.039
171	1630	152	39	F	-		-	-
173	1630	161	48	M	Gammarus		1	0.012
					Daphnia		716	0.198
174	1630	148	36	F	Chaoborus	P	1	0.002
					Daphnia		85	0.022
175	1630	155	41	F	-		-	-
176	1630	236	146	F	-		-	-
177	1630	127	27	F	Daphnia		69	0.019
178	1630	154	35	F	Daphnia		352	0.089
179	1630	145	34	F	Notonectidae	A	1	0.002
180	1630	178	68	F	-		-	-
181	1830	145	31	F	-		-	-
182	1830	181	68	F	-		-	-
183	1830	136	68	F	Chaoborus	P	3	0.007
184	1830	157	37	F	Daphnia		128	0.023
185	1830	139	31	F	-		-	-
186	1830	162	42	F	Gammarus		1	0.020
189	2030	149	33	F	Tetragoneuria	N	3	1.169
					Gammarus		1	0.003
190	2030	201	89	F	Culaea		1	1.709
					Chaoborus	P	1	0.001
191	2030	141	31	F	Daphnia		68	0.012
192	2030	144	33	F	Gammarus		3	0.038
					Daphnia		141	0.079
193	2030	158	39	F	Orconectes		1	0.105
					Gammarus		1	0.103

Table B-2. Cont'd.

Fish Number	Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
194	2030	166	39	F	Tetragoneuria	N	1	0.206
195	2030	172	60	M	-	-	-	-
196	2030	145	78	F	Tetragoneuria	N	1	0.778
197	2030	162	52	F	Daphnia		113	0.028
198	2030	141	32	F	Daphnia		163	0.075
199	2030	160	47	F	Chaoborus	P	11	0.030
200	2030	144	33	F	Chaoborus	P	1	0.002
					Daphnia		23	0.002
201	2030	156	41	F	-	-	-	-
203	2030	164	57	F	-	-	-	-
204	2030	168	46	F	Tetragoneuria	N	1	0.271
205	2030	150	38	F	Notonectidae	A	1	0.058
206	2230	141	32	F	Daphnia		125	0.054
207	2230	147	35	F	Daphnia		172	0.026
208	2230	159	47	F	-	-	-	-
209	2230	151	36	-	Gammarus		2	0.079
210	2230	153	39	F	Chaoborus	P	1	0.003
211	2230	153	52	F	Eucalia		1	0.165
212	2230	159	44	F	-	-	-	-
213	2230	169	48	F	Chaoborus	P	1	0.004
214	2230	145	35	F	Daphnia		81	0.020
215	2230	163	51	F	Daphnia		197	0.046
216	2230	262	175	F	Eucalia		2	1.775

L = Larvae; P = Pupae; N = Nymph; A = Adult.
= Consumed previous day.

Table B-3. Summary of stomach analysis and data from individual fish for the diurnal netting experiment conducted on July 23-24, 1969.

Fish Number	Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
540	0630	150	37	F	-		-	-
541	0630	180	62	M	-		-	-
542	0630	172	54	F	Notonectidae		1	0.002
543	0830	154	44	F	Culaea		1	0.394
					Tetragoneuria	N	2	0.334
544	0830	145	37	F	Culaea		1	0.857
545	1030	151	41	F	Culaea		1	1.233
					Gammarus		1	0.027
546	1030	162	47	F	Gammarus		7	0.101
547	1030	141	32	F	Tetragoneuria		2	1.592
468	1030	172	52	F	-		-	-
469	1030	180	67	F	-		-	-
470	1030	174	58	F	-		-	-
471	1030	161	42	F	Gammarus		7	0.069
472	1030	153	41	F	Chaoborus	P	1	0.001
473	1030	147	38	F	-		-	-
474	1030	162	49	F	Culaea		4	2.274
					Notonectidae		3	0.007
475	1030	152	37	M	-		-	-
476	1030	144	32	-	Gammarus		3	0.063
					Chaoborus	P	1	0.002
477	1030	164	50	F	Perca		2	0.057
485	1230	205	92	F	-		-	-
486	1230	190	91	F	-		-	-
487	1230	192	82	F	Orconectes		1	1.350
					Notonectidae		2	0.009
488	1230	173	49	F	-		-	-
490	1230	143	31	F	Hyalella		8	0.029
					Gammarus		19	0.363
491	1230	159	43	F	Notonectidae		2	0.011
					Gammarus		8	0.113
492	1230	147	35	F	Perca		1	0.962
					Gammarus		1	0.007
493	1230	156	39	F	Perca		1	0.422
494	1230	148	36	F	-		-	-
495	1230	167	54	F	Perca		1	0.228
					Gammarus		1	0.039
496	1230	143	34	F	Culaea		3	0.466
					Notonectidae		3	0.017
					Hyalella		1	0.002
497	1230	221	125	F	Orconectes		1	0.233
					Tetragoneuria	N	2	0.289
498	1230	207	98	F	-		-	-
499	1230	218	113	M	Tetragoneuria	N	1	0.039
500	1430	184	79	F	Orconectes		1	1.900

Table B-3. Cont'd.

Fish Number	Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
501	1430	205	98	F	-		-	-
502	1430	201	93	F	-		-	-
503	1430	209	98	F	Notonectidae		1	0.015
504	1430	217	105	M	Culaea		1	0.157
505	1430	161	48	F	-		-	-
506	1430	148	37	F	Orconectes		1	0.087
507	1430	217	111	F	-		-	-
508	1630	188	67	F	Culaea		2	0.297
509	1630	156	40	F	-		-	-
510	1630	188	72	F	Culaea		1	0.700
511	1630	152	37	F	-		-	-
512	1630	200	76	F	Culaea		1	0.390
513	1630	158	40	M	Notonectidae		2	0.005
					Chaoborus	P	1	0.003
514	1630	150	37	F	Orconectes		1	0.129
515	1630	196	90	M	-		-	-
516	1630	222	120	M	Gastropoda		1	0.009
518	1630	238	144	F	-		-	-
519	1830	194	83	F	-		-	-
520	2030	225	127	F	-		-	-
521	2030	210	97	F	-		-	-
522	2030	207	108	F	Orconectes		2	2.115
523	2030	223	125	F	-		-	-
524	2030	160	49	F	Orconectes		1	0.771
525	2030	201	101	M	Gammarus		15	0.327
526	2030	214	-	F	-		-	-
527	2230	205	109	F	Gammarus		4	0.079
528	2230	186	84	M	Gammarus		9	0.115
529	2230	206	118	M	Gammarus		5	0.094
530	2230	227	138	F	Gammarus		1	0.039
531	2230	198	93	M	Gammarus		9	0.147
532	2230	203	102	F	Gammarus		12	0.402
					Gastropoda		2	0.053
533	2230	227	122	F	-		-	-
534	2230	209	88	F	Notonectidae		2	0.028
					Gammarus		3	0.028
535	2230	221	118	F	Orconectes		1	0.322
536	2230	198	98	F	-		-	-
537	2230	200	96	M	Gammarus		1	0.004
538	2230	163	45	F	-		-	-
539	2230	167	52	F	Gammarus		9	0.344
					Culaea		1	0.132
					Tetragoneuria	N	1	0.159

L = Larvae; P = Pupae; N = Nymph; A = Adult.

Table B-4. Summary of stomach analysis and data from individual fish for the diurnal netting experiment conducted on August 24-25, 1969.

Fish Number	Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
844	0830	187	82	M	-		-	-
845	0830	219	124	F	Perca		1	0.558
846	0830	207	96	F	-		-	-
847	0830	210	105	F	Perca		2	1.037
848	0830	215	128	F	-		-	-
849	0830	164	62	M	Orconectes		1	3.242
800	1030	155	39	F	Gammarus		32	0.076
801	1030	162	45	F	Culaea		2	0.324
802	1030	186	65	F	-		-	-
803	1030	150	35	F	Culaea		1	0.090
					Hyalella		21	0.060
804	1030	183	64	F	-		-	-
805	1030	155	40	F	Orconectes		1	0.065
					Gammarus		84	0.265
806	1030	176	58	F	Hyalella		8	0.013
					Gammarus		21	0.218
807	1030	160	42	F	Orconectes		1	0.026
808	1030	143	36	F	Culaea		2	0.601
809	1030	171	52	F	Culaea		1	0.349
810	1230	159	43	F	Amphipoda		-	0.014
811	1230	146	35	F	Hyalella		2	0.008
					Gammarus		2	0.035
					Chaoborus	L	2	0.003
812	1230	152	38	F	Gammarus		84	0.287
813	1230	152	34	F	Gastropoda		1	0.006
814	1230	148	37	F	Hyalella		1	0.002
					Culaea		1	0.063
814-A	1230	153	42	M	Gastropoda		2	0.002
					Gammarus		19	0.068
815	1230	150	39	F	-		-	-
816	1230	154	39	M	-		-	-
817	1230	148	35	F	-		-	-
818	1430	155	38	F	Gammarus		4	0.068
					Hyalella		17	0.045
819	1430	150	35	F	-		-	-
820	1430	199	87	F	-		-	-
821	1830	207	97	F	Culaea		1	0.100
822	1830	146	34	F	-		-	-
823	1830	148	35	F	-		-	-
824	1830	153	36	F	-		-	-
825	1830	165	46	F	-		-	-
826	1830	172	53	F	-		-	-
827	1830	220	110	F	Tetragoneuria	N	1	0.285
828	2030	159	40	F	-		-	-
829	2030	156	37	F	-		-	-

Table B-4. Cont'd.

Fish Number	Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
830	2030	152	39	F	-		-	-
831	2030	157	40	F	Orconectes		1	0.077
832	2030	153	36	F	Culaea		2	0.267
833	2030	152	35	F	Culaea		2	0.109
834	2030	207	99	F	Orconectes		1	2.614
					Hymenoptera		1	0.044
835	2030	152	36	F	-		-	-
836	2030	164	47	F	-		-	-
837	2030	157	42	F	-		-	-
838	2030	152	39	M	-		-	-
839	2230	161	47	M	Daphnia		83	0.039
840	2230	146	37	F	Hyalella		7	0.018
					Daphnia		376	0.151
841	2230	156	40	M	Culaea		1	0.170
842	2230	153	38	F	-		-	-
843	2230	151	36	M	-		-	-

L = Larvae, P = Pupae, A = Adult, N = Nymph.

Table B-5. Summary of stomach analysis and data from individual fish for the diurnal netting experiment conducted on June 23-24, 1970.

Fish Number	Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
28	0630	71	4	F	-		-	-
29	0630	65	3	M	-		-	-
30	0630	55	3	M	-		-	-
31	0630	60	3	F	Chaoborus	P	2	0.005
					Hyalella		1	0.017
					Daphnia		10	0.002
32	0630	65	3	M	Notonectidae	A	5	0.022
80	0830	78	6	F	Hyalella		1	0.009
					Daphnia		146	0.056
81	0830	84	7	M	Daphnia		20	0.012
82	0830	66	4	F	Daphnia		278	0.073
83	0830	71	5	F	Gammarus		3	0.113
					Chaoborus	L	1	0.002
					Daphnia		75	0.018
50	1030	71	4	F	Daphnia		172	0.062
					Hyalella		1	0.013
51	1030	68	4	F	Chaoborus	P	1	0.002
					Diptera	L	1	-
					Daphnia		126	0.050
52	1030	68	4	F	Hyalella		1	0.009
					Daphnia		128	0.074
53	1030	68	4	F	Chaoborus	P	14	0.029
					Chaoborus	L	2	0.003
					Hyalella		1	0.010
					Perca		1	0.017
					Daphnia		84	0.034
					Notonectidae	A	1	0.019
54	1030	71	5	M	Chaoborus	P	2	0.006
					Perca		2	0.019
					Hyalella		1	0.009
					Daphnia		89	0.026
55	1030	97	9	F	Gammarus		3	0.035
					Hyalella		3	0.024
					Chaoborus		2	0.009
					Daphnia		37	0.054
					Notonectidae	A	2	0.021
6	1030	72	5	F	Daphnia		276	0.072
7	1030	72	5	M	Chaoborus	P	4	0.007
					Daphnia		25	0.011
8	1030	88	8	M	Daphnia		99	0.026
9	1030	69	4	M	Daphnia		186	0.052
10	1030	67	4	M	Chaoborus	p	19	0.040
					Perca		2	0.017
					Daphnia		30	0.074

Table B-5. Cont'd.

Fish Number	Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
87	1030	80	6	M	Hyalella		8	0.032
					Chaoborus	P	1	0.005
					Daphnia		35	0.004
89	1030	82	7	M	Daphnia		67	0.027
					Chironomidae	P	1	0.001
90	1030	73	5	M	Culaea		1	0.070
91	1030	88	6	F	-		-	-
92	1030	81	8	F	Daphnia		39	0.020
93	1030	53	2	F	Chaoborus	P	14	0.054
					Chaoborus	L	1	0.001
94	1030	75	6	F	Daphnia		31	0.016
33	1430	84	8	M	-		-	-
34	1430	76	6	F	Gammarus		2	0.039
35	1430	76	6	M	Gammarus		1	0.025
					Chaoborus		2	0.005
					Ephemeroptera	N	1	0.014
					Daphnia		43	0.040
36	1430	70	4	M	Chaoborus	P	6	0.024
					Daphnia		70	0.049
56	1630	-	4	F	Chaoborus	P	1	0.002
					Amphipod		1	0.004
57	1630	-	2	M	Chaoborus	P	1	0.002
58	1630	-	2	F	-		-	-
59	1630	-	3	M	-		-	-
60	1630	71	5	F	Daphnia		105	0.043
61	1630	71	5	F	Daphnia		118	0.062
62	1630	70	5	M	Notonectidae	A	1	0.009
					Daphnia		50	0.022
63	1630	80	6	F	Chaoborus	P	1	0.003
					Plecoptera	N	1	0.012
					Daphnia		20	0.005
72	1630	71	5	M	Hyalella		8	0.028
					Notonectidae	A	2	0.004
73	1630	68	4	F	Gammarus		3	0.037
					Hyalella		1	0.010
					Notonectidae	A	1	0.022
74	1630	88	7	F	Daphnia		1	0.008
					Chaoborus	P	7	0.003
75	1630	84	7	F	Gammarus		1	0.029
					Hyalella		1	0.008
					Chaoborus	P	1	0.003
					Daphnia		20	0.002
76	1630	66	4	F	Gammarus		1	0.028
77	1630	71	5	F	Hyalella		9	0.041
11	1830	73	6	M	Daphnia		59	0.009
					Chironomidae	P	1	0.001

Table B-5. Cont'd.

Fish Number	Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
12	1830	78	6	F	Gammarus		2	0.019
					Hyalella		3	0.026
					Chironomidae	P	2	0.004
					Daphnia		27	0.006
13	1830	70	5	F	Gammarus		1	0.009
					Hyalella		8	0.024
					Notonectidae	A	2	0.016
					Daphnia		37	0.021
					Perca		1	0.025
14	1830	67	4	M	Daphnia		31	0.007
					Chironomid	P	1	0.001
64	1830	96	13	M	Daphnia		94	0.031
65	1830	103	14	F	Chaoborus	P	30	0.112
70	1830	67	4	F	Gammarus		2	0.023
					Notonectidae	A	1	0.019
					Daphnia		9	0.001
37	2030	67	4	F	Hyalella		9	0.031
					Perca		1	0.009
38	2030	65	3	M	-		-	-
15	2030	60	4	M	Daphnia		143	0.056
					Chaoborus		1	0.002
16	2030	68	4	F	Daphnia		40	0.014
17	2030	89	9	F	Daphnia		32	0.010
18	2030	68	4	F	Daphnia		32	0.012
19	2030	65	4	F	Daphnia		63	0.030
48	2030	80	7	M	Daphnia		75	0.021
1	2230	65	4	M	Hyalella		8	0.028
2	2230	59	3	F	Chironomidae	P	1	0.002
					Diptera	P	1	T
					Daphnia		67	0.011
3	2230	60	3	M	Chironomid	P	1	T
					Daphnia		81	0.008
4	2230	58	2	F	Chironomidae	P	1	0.002
					Daphnia		76	0.013
5	2230	55	2	F	Chironomidae	P	7	0.008
					Daphnia		78	0.009
24	2230	60	3	F	-		-	-
25	2230	68	4	F	Hyalella		5	0.030
					Chaoborus	P	1	0.002
26	2230	62	3	-	Hyalella		4	0.029
					Gammarus		1	0.020
67	2430	79	6	M	Chaoborus	P	5	0.013
					Chaoborus	L	1	0.001
					Hyalella		1	0.009
					Daphnia		22	0.015

Table B-5. Cont'd.

Fish Number	Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
66	2430	88	9	M	Gammarus		1	0.027
					Chaoborus	P	1	0.003
68	2430	61	3	F	Gammarus		1	0.005
					Hyalella		1	0.003
					Daphnia		17	0.001
69	2430	60	3	F	-		-	-

L = Larvae, P = Pupae, N = Nymph, A = Adult.
T = Trace.

Table B-6. Summary of stomach analysis and data from individual fish for the diurnal netting experiment conducted on July 21-22, 1970.

Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
0630	75	5	F	-		-	-
0630	86	7	M	-		-	-
0630	76	6	M	-		-	-
0630	71	5	M	-		-	-
0630	75	5	M	-		-	-
0630	74	5	M	-		-	-
0630	84	8	F	Perca		1	0.032
0630	84	8	F	-		-	-
0630	86	8	M	-		-	-
0630	78	6	M	-		-	-
0630	75	6	M	-		-	-
0630	77	6	F	-		-	-
0630	77	7	F	-		-	-
0830	76	6	M	-		-	-
0830	76	6	M	-		-	-
0830	71	5	F	Hyalella		3	0.016
				Gammarus		1	0.013
0830	76	5	F	Hyalella		4	0.006
0830	76	5	F	Hyalella		9	0.019
				Chironomidae	P	1	0.001
0830	80	7	M	-		-	-
0830	75	5	M	Hyalella		10	0.005
0830	80	7	F	Perca		1	0.148
0830	80	6	F	Orconectes		1	0.035
				Notonectidae	A	5	0.010
				Gammarus		4	0.004
				Hyalella		12	0.021
0830	81	7	M	Chironomidae	P	1	0.002
				Hyalella		4	0.019
0830	100	15	F	Perca		1	0.171
0830	90	10	M	Perca		4	0.379
0830	75	6	F	Perca		3	0.413
1030	113	19		Ephemeroptera	N	1	0.001
				Perca		3	0.069
				Hyalella		2	0.005
1030	80	7		Gammarus		3	0.017
				Hyalella		9	0.043
				Diptera	L	1	0.001
1030	78	6		Gammarus		9	0.030
				Hyalella		31	0.049
				Diptera	P	1	0.001
1030	83	7		Gammarus		4	0.021
				Hyalella		18	0.079
1030	81	6		-		-	-

Table B-6. Cont'd.

Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
1030	101	14		Hyalella		29	0.181
				Gammarus		11	0.103
1030	85	8		Hyalella		58	0.116
				Gammarus		13	0.058
1030	84	8		Hyalella		25	0.090
				Gammarus		5	0.049
1030	111	19		-		-	-
1030	101	14		Gammarus		14	0.202
				Debris		1	0.003
				Hyalella		5	0.025
1030	81	8		Perca		1	0.163
1030	81	7		Gammarus		6	0.083
				Hyalella		19	0.050
1230	73	6		Hyalella		2	0.008
				Gammarus		24	0.073
1230	77	6		Hyalella		17	0.042
				Gammarus		24	0.098
1230	76	5		Hyalella		33	0.065
				Gammarus		7	0.035
1230	117	22		Hyalella		83	0.154
				Gammarus		11	0.187
1230	73	5	M	Hyalella		14	0.026
				Gammarus		1	0.010
1230	81	7	M	Hyalella		30	0.049
				Gammarus		5	0.025
				Diptera	L	2	0.002
1230	78	6	M	Hyalella		20	0.044
1230	85	8	M	Gammarus		5	0.024
				Hyalella		8	0.081
1230	87	13	F	Perca		2	0.087
				Hyalella		2	0.011
1230	71	5	M	Hyalella		14	0.021
				Gammarus		6	0.019
				Notonectidae	A	1	0.002
1430	75	6	M	Gammarus		1	0.010
				Hyalella		16	0.036
1430	76	6	F	Gammarus		1	0.005
				Hyalella		5	0.019
1430	103	14	M	Gammarus		3	0.025
				Hyalella		25	0.085
1430	90	11	F	Ephemeroptera	N	1	0.004
				Hyalella		70	0.148
				Gammarus		6	0.048
1430	81	7	M	Hyalella		11	0.025
1430	76	6	F	Gammarus		1	0.011
				Hyalella		5	0.019

Table B-6. Cont'd.

Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
1430	96	11	M	Hyalella		21	0.021
				Gammarus		9	0.037
				Notonectidae	A	1	0.002
1430	67	5	M	Notonectidae	A	1	0.001
1430	75	5	M	Gammarus		1	0.030
				Hyalella		1	0.003
1430	76	6	F	Perca		2	0.088
1430	81	7	M	Hyalella		3	0.009
1430	74	5	M	Perca		1	0.069
1430	73	5	M	Hyalella		4	0.017
1630	98	12	F	Orconectes		1	0.020
				Notonectidae	A	1	0.002
				Gammarus		11	0.013
1630	73	5	M	Plecoptera	N	1	0.001
				Gammarus		19	0.017
1630	75	6	M	Notonectidae	A	1	0.002
				Gammarus		12	0.020
				Hyalella		2	0.006
1630	102	14	M	Hyalella		11	0.014
				Gammarus		6	0.035
				Diptera	L	1	0.001
1630	76	14	M	Hyalella		11	0.022
				Gammarus		1	0.008
1630	82	6	F	Notonectidae	A	1	0.008
1630	93	7	F	Hyalella		30	0.012
				Gammarus		10	0.050
1630	77	11	M	-		-	-
1630	71	6	F	Gammarus		2	0.013
				Hyalella		23	0.032
1630	101	5	F	Gammarus		4	0.013
1630	77	6	F	Hyalella		10	0.019
				Gammarus		9	0.043
1630	70	5	M	Hyalella		39	0.137
1830	77	6	M	-		-	-
1830	83	7	M	Hyalella		33	0.120
				Gammarus		10	0.030
1830	79	6	M	Hyalella		26	0.082
				Diptera	L	1	0.001
1830	80	7	M	Hyalella		54	0.155
				Gammarus		3	0.017
1830	71	5	M	Hyalella		19	0.059
				Gammarus		1	0.005
1830	72	5	F	Hyalella		34	0.121
1830	71	5	M	Hyalella		6	0.035
1830	81	7	F	Hyalella		16	0.095
				Gammarus		2	0.006

Table B-6. Cont'd.

Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
1830	74	5	F	Hyalella		13	0.068
2030	81	7	M	Hyalella		6	0.026
2030	82	7	M	-		-	-
2030	72	5	M	Hyalella		9	0.034
				Chironomidae	P	1	0.001
2030	74	5	F	Chaoborus	L	1	0.001
				Hyalella		29	0.098
2030	79	6	M	-		-	-
2030	81	7	F	Hyalella		8	0.052
				Notonectidae		4	0.013
2030	76	6	F	Hyalella		19	0.039
				Gammarus		2	0.021
2230	84	9	F	Hyalella		10	0.027
2230	88	9	F	Hyalella		6	0.027
				Gammarus		2	0.004
2230	74	5	F	-		-	-
2230	74	6	M	Hyalella		6	0.011
2230	85	8	F	Perca		1	0.283
2230	85	8	F	-		-	-
2230	71	5	M	Hyalella		19	0.067
2230	83	8	F	Hyalella		8	0.013
2230	75	6	F	Diptera	L	1	0.001
				Hyalella		28	0.088
				Gammarus		3	0.021
2230	80	7	M	-		-	-
2230	73	5	M	Hyalella		24	0.048
2230	81	7	F	-		-	-
2230	78	6	F	-		-	-
2230	71	5	F	Perca		1	0.027
2230	74	5	M	Perca		1	0.177
2230	107	17	M	Gammarus		3	0.017
				Chaoborus	L	1	0.002
2230	105	16	M	-		-	-
2230	112	18	M	-		-	-
2230	107	18	F	-		-	-
2230	93	11	F	-		-	-
2230	101	16	F	-		-	-
2230	96	13	F	-		-	-
2230	103	14	M	-		-	-
2230	78	6	M	Hyalella		1	0.002
2230	76	6	F	Hyalella		9	0.037
2230	77	6	F	Perca		1	0.116
2230	83	7	F	Ephemeroptera	N	1	0.002
				Hyalella		15	0.084
				Gammarus		1	0.010

Table B-6. Cont'd.

Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
2230	76	7	M	Hyalella		29	0.109
				Gammarus		7	0.070
2230	82	7	M	Hyalella		20	0.050
				Gammarus		2	0.023
2230	77	6	M	Hyalella		1	0.005
2230	76	6	F	Hyalella		11	0.021
2230	79	6	F	Perca		1	0.129
				Diptera	P	5	0.005
				Hyalella		20	0.078
2230	81	7	M	Diptera	P	1	0.001
				Hyalella		30	0.074
2230	80	6	F	Hyalella		13	0.070
				Ephemeroptera	N	1	0.002
				Diptera	P	1	0.001
2230	78	6	M	Hyalella		10	0.049

L = Larvae, P = Pupae, N = Nymph, A = Adult.

T = Trace.

Table B-7. Summary of stomach analysis and data from individual fish for the diurnal netting experiment conducted on August 24-26, 1970.

Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
0630	112	19	F	-		-	-
0630	98	12	F	Orconectes		1	0.024
0630	92	13	F	-		-	-
0630	95	11	M	-		-	-
0830	100	13	M	Notonectidae	A	1	0.012
0830	102	14	F	-		-	-
0830	104	13	M	-		-	-
1230	91	9	M	-		-	-
1230	89	8	F	Hyalella		3	0.012
1230	88	7	M	Hyalella		30	0.026
1230	88	8	F	Hyalella		1	0.001
1230	95	9	M	-		-	-
1230	79	6	M	Hyalella		12	0.013
1230	75	4	F	Orconectes		1	0.043
				Tetragoneuria	N	1	0.007
				Plecoptera	N	1	0.001
1230	82	7	F	-		-	-
1230	89	9	F	Gammarus		3	0.011
				Hyalella		2	0.021
1230	82	7	M	-		-	-
1230	89	8	F	-		-	-
1230	114	17	F	-		-	-
1830	101	13	M	Culaea		1	0.057
1830	93	10	F	Culaea		1	0.537
1830	96	11	M	Hyalella		53	0.059
				Gammarus		6	0.021
				Diptera	L	1	0.001
2030	104	13	M	Tetragoneuria	N	1	0.090
2030	104	13	F	Hyalella		17	0.027
				Gammarus		3	0.053
2030	92	10	M	Gammarus		2	0.017
				Hyalella		25	0.073
2030	103	13	F	-		-	-
2030	93	10	M	Hyalella		23	0.032
2030	95	11	M	Gammarus		2	0.010
				Hyalella		3	0.009
2030	95	11	M	Orconectes		1	0.253
2030	96	10	M	Hyalella		4	0.014
2030	86	9	F	Hyalella		27	0.020
2030	90	8	M	Hyalella		37	0.010
				Gammarus		2	0.010
2030	89	9	M	Hyalella		1	0.013
				Gammarus		9	0.031
2030	96	11	M	Culaea		2	0.319
2030	109	16	F	Culaea		1	0.257

Table B-7. Cont'd.

Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
2030	91	9	M	Hyalella		25	0.019
2030	89	9	M	Perca		1	1.300
2030	100	13	F	Hyalella		40	0.033
				Debris		-	0.006
2030	87	9	M	Gammarus		3	0.042
2030	99	12	F	Hyalella		60	0.069
2030	86	9	F	Hyalella		81	0.100
2030	87	8	M	Gammarus		6	0.030
				Hyalella		36	0.042
2030	89	9	M	Hyalella		45	0.048
				Diptera	L	5	0.005
2030	89	9	F	Hyalella		38	0.042
				Gammarus		4	0.027
				Tetragoneuria	N	1	0.006
2030	105	13	M	Gammarus		6	0.077
				Hyalella		3	0.009
2030	99	11	F	Culaea		1	0.045
2030	98	8	M	-		-	-
2030	92	9	M	-		-	-
2030	96	8	F	-		-	-

L = Larve, P = Pupae, N = Nymph, A = Adult.

Table B-8. Summary of stomach analysis and data from individual fish for the diurnal netting experiment conducted on September 14-16, 1970.

Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
0830	71	5	M	Daphnia		9	0.001
0830	71	5	M	Daphnia		46	0.008
				Chaoborus	L	3	0.001
0830	68	4	M	Daphnia		35	0.005
0830	66	4	M	Daphnia		67	0.011
0830	72	5	F	Daphnia		31	0.014
0830	71	5	M	Daphnia		28	0.011
0830	94	10	M	-		-	-
0830	99	11	M	-		-	-
0830	96	11	M	-		-	-
0830	99	12	M	-		-	-
1030	77	6	M	-		-	-
1030	68	4	F	Daphnia		37	0.103
1030	70	4	M	Daphnia		110	0.038
				Chaoborus	L	5	0.002
1030	70	5	M	Hyalella		36	0.046
				Chironomidae	L	1	0.003
				Daphnia		26	0.005
				Ostracoda		1	T
1030	94	13	M	Daphnia		70	0.031
1230	70	4	M	Gammarus		2	0.015
				Daphnia		76	0.036
1230	73	5	M	Hyalella		1	0.006
				Daphnia		134	0.040
1230	75	5	M	Daphnia		206	0.061
				Chaoborus	L	1	0.001
1230	70	5	M	Daphnia		120	0.036
1230	67	4	M	Daphnia		65	0.013
1230	70	4	M	Daphnia		68	0.009
1230	75	5	M	Daphnia		379	0.086
1230	71	5	M	Daphnia		427	0.091
1230	71	5	M	Daphnia		93	0.030
1230	72	4	M	Daphnia		25	0.006
1230	69	4	M	Chironomidae	P	1	0.001
				Gammarus		1	0.007
				Daphnia		120	0.034
1230	82	8	M	Culaea		1	0.029
1230	99	12	M	-		-	-
1430	72	5	M	Gammarus		11	0.124
				Chironomidae	P	1	0.001
1430	73	4	F	Daphnia		175	0.053
1430	69	4	M	Chironomidae	L	1	0.001
				Chaoborus	L	2	0.002
				Gammarus		4	0.078
				Hyalella		2	0.017
				Daphnia		7	0.002

Table B-8. Cont'd.

Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
1430	76	6	F	Daphnia		1025	0.212
1430	64	4	F	Daphnia		397	0.087
1430	63	4	F	Daphnia		417	0.093
1430	73	4	M	Hyalella		1	0.007
				Daphnia		276	0.057
1430	69	4	F	Gammarus		4	0.039
				Hyalella		2	0.012
1430	69	4	M	Daphnia		192	0.053
1430	65	4	M	Chaoborus	L	1	0.001
				Daphnia		239	0.071
1430	84	8	M	Gammarus		2	0.033
1630	69	4	M	Daphnia		146	0.051
1630	68	4	M	Daphnia		176	0.050
1630	70	4	M	Daphnia		88	0.028
1630	68	4	M	Daphnia		279	0.072
1630	69	4	M	Gammarus		2	0.021
1630	70	4	M	Daphnia		331	0.090
1630	76	6	M	Gammarus		3	0.010
				Hyalella		5	0.013
				Daphnia		12	0.007
1630	71	5	M	Gammarus		2	0.030
				Hyalella		1	0.005
1630	75	5	M	Gammarus		2	0.049
1630	74	5	M	Chironomidae	L	2	0.002
				Hyalella		5	0.023
1830	71	4	M	Daphnia		350	0.084
1830	68	4	F	Daphnia		217	0.067
1830	72	5	M	Hyalella		10	0.024
				Daphnia		12	0.006
1830	73	5	M	Gammarus		1	0.019
				Daphnia		27	0.003
1830	69	4	F	Daphnia		297	0.079
1830	72	4	M	Daphnia		37	0.017
1830	75	5	M	Daphnia		243	0.061
1830	74	5	M	Daphnia		411	0.086
1830	96	11	M	Daphnia		197	0.040
1830	95	11	M	Daphnia		183	0.049
1830	110	15	F	Daphnia		251	0.069
1830	100	13	F	Daphnia		897	0.173
1830	102	13	F	Daphnia		210	0.057
2030	73	5	F	Daphnia		251	0.071
2030	71	5	M	Daphnia		175	0.040
2030	69	4	M	Daphnia		411	0.099
2030	77	5	M	Daphnia		517	0.118
2030	69	4	F	Daphnia		376	0.090
2030	68	4	F	Daphnia		236	0.078

Table B-8. Cont'd.

Time Caught	Fork Length (mm)	Weight (g)	Sex	Food Organism	Type	Number	Weight (g)
2030	71	4	M	Daphnia		221	0.075
				Chaoborus	L	1	0.001
2030	74	5	M	Daphnia		341	0.094
2030	67	4	F	Daphnia		279	0.100
2030	67	4	M	Chironomidae	L	1	0.001
				Daphnia		260	0.054
				Gammarus		1	0.010
2030	70	4	M	Daphnia		93	0.027
2030	71	4	F	Chironomidae	L	1	0.001
				Hyalella		7	0.017
				Daphnia		25	0.008
2030	98	12	M	Daphnia		257	0.076
2030	100	12	M	-		-	-
2030	95	11	F	Daphnia		1079	0.272
2030	105	16	M	Orconectes		1	0.600
2030	90	10	M	Gammarus		1	0.017
				Daphnia		319	0.124
2230	70	5	M	Daphnia		497	0.127
2230	79	6	M	Daphnia		197	0.070
2230	71	5	M	Daphnia		210	0.088
2230	102	13	M	-		-	-
2230	95	10	M	Culaea		1	0.038
2230	95	10	M	-		-	-
2230	97	12	M	Chironomidae	L	1	0.001
				Hyalella		16	0.053
				Daphnia		27	0.016

L = Larve, P = Pupae, N = Nymph, A = Adult.
T = Trace.

APPENDIX C

Table C-1. Summary of stomach analysis carried out on adult perch from areas different from 1969 diurnal nettings.

	June - Basin I *Chara* Beds		August - Basin II *Potamogeton* & *Ranunculus*	
	[12]	(4)	[17]	(2)
Foor Organisms	% No.	% Wt.	% No.	% Wt.
Crustacea	54.2	40.1	97.4	57.8
Cladocera	-	-	9.1	0.7
Daphnia	-	-	9.1	0.7
Amphipoda	51.8	18.2	87.9	43.0
Hyalella	10.8	0.7	70.7	25.3
Gammarus	41.0	17.5	17.2	17.7
Decapoda	2.4	22.9	0.4	14.1
Orconectes	2.4	22.9	0.4	14.1
Insecta	31.2	8.6	1.6	9.9
Diptera	20.4	0.7	-	-
Chaoborinae(P)	20.4	0.7	-	-
Odonata(N)	2.4	6.6	-	-
Hemiptera(A)	8.4	1.3	1.6	9.9
Corixidae	8.4	1.3	1.6	9.9
Hydracarina	-	-	-	-
Hirudina	-	-	-	-
Fish	14.4	50.9	1.0	29.3
Perca	12.0	30.2	-	-
Eucalia	2.4	20.7	1.0	29.3
Debris	-	-	-	3.0

[ ] = No. of Fish ( ) = No. of Empty Stomachs

A = Adult P = Pupae N = Nymph

Table C-2. Summary of data for the relationship between stomach content weight (S) and fish length (L) using all perch from 1969 and 1970.

Fork Length Interval (mm)	No. of Fish	$\bar{X}_L$ (mm)	$\bar{X}_S$ (g)	CI(P = 0.95) $\pm$	In $\bar{X}_L$	In $\bar{X}_S$ X 10^3
50-59	5	56.0	0.0324	0.0275	4.0253	3.4780
60-69	27	65.8	0.0413	0.0136	4.1865	3.7209
70-79	97	74.3	0.0688	0.0127	4.3081	4.2312
80-89	47	82.7	0.0717	0.0189	4.4151	4.2724
90-99	34	94.5	0.1882	0.0932	4.5485	5.2376
100-109	19	102.6	0.1056	0.0410	4.6307	4.6597
110-119	10	115.7	0.2203	0.2531	4.7509	5.3949
140-149	26	144.9	0.2805	0.1702	4.9761	5.6367
150-159	33	154.2	0.1840	0.0903	5.0382	5.2148
160-169	30	164.1	0.3615	0.2570	5.1004	5.8902
170-179	11	175.1	0.2881	0.1987	5.1651	5.6634
180-189	12	185.0	0.5185	0.3291	5.2204	6.2513
190-199	6	194.8	0.4303	0.5556	5.2719	6.0645
200-209	16	204.7	0.5406	0.4435	5.3191	6.2927
210-	19	230.8	1.2792	1.4388	5.4414	7.9344

Table C-3. Summary of data from the digestion rate experiments conducted on adult perch during 1969 and 1970.

Amphipods (11.5-13.5 C)		Amphipods (16 C)		Stickleback (15 C)		Crayfish (20 C)	
Time(Hrs)	% Digestion	Time(Hrs)	% Digestion	Time(Hrs)	% Digestion	Time(Hrs)	% Digestion
1.7	17.9	0.1	0.1	8	6.2	6	- 1.
2.8	21.4	2.2	7.4	8	12.5	6	2.1
3.2	26.1	3.6	12.4				
3.7	44.2	4.2	27.1	15	27.1	16	2.8
4.7	74.6	4.8	61.8	15	45.5	16	5.1
5.7	93.6	4.9	40.1			32	- 1.
6.0	81.9	5.5	36.2	19	44.0	32	36.5
6.3	97.9	5.5	37.6	19	53.1		
6.7	47.9	5.3	46.0				
7.1	91.7	6.4	64.4	28	56.2	44	55.5
7.3	95.2	6.4	89.7	28	88.0	44	80.1
7.3	81.9	8.6	68.2				
7.4	100.0	9.1	94.0	38	94.2	55	93.3
8.2	95.2	9.6	56.7	38	98.8		
9.3	89.1	10.1	68.6			55	- 1.
9.8	89.6	10.4	74.1			64	98.4
10.5	74.6	10.6	84.3				
10.7	88.1	12.9	83.8			64	- 1.
11.4	94.5	13.1	100.0				
11.8	91.8						

1. = Regurgitation

Table C-4. Summary of data from the digestion rate experiment conducted on juvenile perch for June, 1970 ($\bar{X}$ = stomach content weight per unit fish weight).

Time (Hrs)	No. of Perch	$\bar{X}$	Range	C.I.(P = 0.95) ±	In $\bar{X}$ X10^4
0.0	7	0.01888	0.00993-0.02791	0.00776	5.2406
4.5	5	0.01355	0.00813-0.02319	0.00682	4.9088
6.0	4	0.01012	0.0 - 0.01659	0.01190	4.6169
7.0	5	0.00826	0.00408-0.01000	0.00297	4.4140
7.5	5	0.00818	0.00526-0.01083	0.00344	4.4039
10.0	4	0.00579	0.00589-0.00760	0.00257	4.0578
10.5	5	0.00524	0.00027-0.01050	0.00416	3.9585
11.5	4	0.00425	0.0 - 0.00746	0.00493	3.7497
15.0	3	0.00311	0.00026-0.00714	0.00891	3.4379
16.0	2	0.00304	0.00282-0.00326	0.00279	3.4144
17.5	3	0.00180	0.0 - 0.00315	0.00404	2.8904
21.5	6	0.00091	0.0 - 0.00543	0.00234	2.8904
23.0	6	0.00080	0.0 - 0.00270	0.00113	2.0806
25.5	7	0.00028[1.]	0.0 - 0.00193	0.00068	-
31.0	5	0 [1.]	-	-	-

1. = Not used in regression analysis.

Table C-5. Summary of data from the digestion rate experiment conducted on juvenile perch for July, 1970. ($\bar{X}$ = Stomach content weight per unit fish weight.)

Time (Hrs)	No. of Perch	$\bar{X}$	Range	C.I.(P = 0.95) ±	In $\bar{X}$ X10^4
0.0	7	0.01353	0.0 - 0.02148	0.00666	4.9050
6.5	7	0.00800	0.0 - 0.0170	0.00506	4.3820
8.0	9	0.00690	0.0 - 0.02567	0.00643	4.2339
10.0	12	0.00421	0.0 - 0.01724	0.00381	3.7391
13.0	6	0.00387	0.0 - 0.00140	0.00615	3.6558
14.0	4	0.00175	0.0 - 0.0050	0.00365	2.8621
17.5	6	0.00133	0.0 - 0.0030	0.00159	2.5901
23.0	6	0.00114	0.0 - 0.0040	0.00208	2.4361
24.5	3	0.00003[1.]	0.0 - 0.0010	0.00142	-
28.0	7	0 [1.]	-	-	-

1. = Not used in regression analysis.

Table C-6. Summary of data from the digestion rate experiment conducted on juvenile perch for September, 1970. ($\bar{X}$ = Stomach content weight per unit fish weight).

Time (Hrs)	No. of Perch	$\bar{X}$	Range	C.I.(P = 0.95) ±	In $\bar{X}$ X10^4
0.0	11	0.02240	0.00434-0.03719	0.00680	5.4114
2.0	13	0.01878	0.00604-0.02663	0.00305	5.2331
6.5	7	0.01373	0.00476-0.02459	0.00619	5.9222
8.5	7	0.01158	0.00522-0.02380	0.00595	4.7343
13.5	7	0.00858	0.00212-0.01411	0.00418	4.4520
17.5	10	0.00729	0.0 - 0.01600	0.00414	4.2890
18.5	6	0.00631	0.0 - 0.02021	0.00748	4.1446
21.0	7	0.00522	0.0 - 0.01025	0.00416	3.9551
24.5	7	0.00475	0.0 - 0.01636	0.00582	3.8607
26.5	6	0.00211[1.]	0.0 - 0.00457	0.00201	-
29.0	6	0.00122[1.]	0.00021-0.00304	0.00108	-
32.0	5	0.00050[1.]	0.0 - 0.00220	0.00122	-
34.0	3	0.00049[1.]	0.0 - 0.00148	0.00211	-
35.0	8	0.00042[1.]	0.0 - 0.00309	0.00091	-
38.5	6	0 [1.]	-	-	-
38.5	7	0 [1.]	-	-	-

1. = Not used in regression analysis.

Table C-7. Summary of data used in calculation of daily consumption for juvenile yellow perch from 1970 diurnal netting experiments. (No. = Number of perch; W/W I = Wt. of stomach contents/fish wt; W/W D = Wt./fish wt. digested; W/W C = Wt./fish wt. consumed.)

	Month											
Time Interval	June			July			August			September		
	No.	W/W I	W/W D	W/W C	No.	W/W I	W/W D	W/W C	No.	W/W I	W/W D	W/W C	No.	W/W I	W/W D	W/W D
0430-0630	5	0.00312	0.00045	0.00359	13	0.00031[1.]	-	-	4	0.00070[1.]	-	-	0	-	-	-
-0830	5	0.01275	0.00226	0.01187	13	0.01284	0.00158	0.01420	3	0.00030	0.00004	0.00034	10	0.00122	0.00008	0.00130
-1030	18	0.01275	0.00362	0.00362	12	0.01349	0.00324	0.00389	0	-	-	-	5	0.00607	0.00047	0.00534
-1230	0	-	-	-	10	0.01252	0.00320	0.00228	12	0.00170	0.00125	0.00190	13	0.00898	0.00096	0.00287
-1430	4	0.00930	0.00626	0.00281	14	0.00718	0.00242	0.0	10	0.00370	0.00066	0.00414	11	0.02240	0.00200	0.01542
-1630	14	0.00561	0.00212	0.0	12	0.00644	0.00167	0.00093	7	0.00950	0.00162	0.00742	10	0.01042	0.00210	0.0
-1830	5	0.00728	0.00183	0.00350	9	0.01548	0.00269	0.01173	3	0.02250	0.00394	0.01694	13	0.01039	0.00133	0.00130
-2030	8	0.00549	0.00181	0.00002	7	0.00702	0.00272	0.0	27	0.01130	0.00416	0.0	17	0.01853	0.00184	0.00998
-2230	11	0.00677	0.00174	0.00202	35	0.00782	0.00178	0.00158	0	-	-	-	7	0.00985	0.00184	0.0
-2430	4	0.00335	0.00144	0.0	0	-	-	-	0	-	-	-	0	-	-	-
Daily consumption $\sum$ =				0.02743				0.03478				0.03079				0.03621
Percentage of body weight =				2.73				3.48				3.08				3.62

1. = From previous day's feeding.

APPENDIX D

Table D-1. Results from Friedman's test used to test for consistency of diurnal capture rate over the seasons sampled.

Year	df	χ_r^2
1969	8	1.737
1970	8	8.015

Table D-2. Results of Bartlett's test used to test for homogeneity of variance within diurnal netting experiments. Analysis was carried out on transformed data.

Netting experiment	df	χ_c^2
June 8-9, 1969	5	56.42*
June 22, 1969	7	44.53*
July, 1969	7	122.58*
August, 1969	6	100.31*
June, 1970	8	149.71*
July, 1970	8	517.84*
August, 1970	6	128.67*
September, 1970	7	121.67*

* = $P < 0.05$

Table D-3. Summary of Kruskall-Wallis test results from comparison within and among netting experiments.

Test Comparison	Date	df	H
Among months	1969	3	19.272*
	1970	3	23.912*
Within months	June 8-9, 1969	4	5.366
	June 22, 1969	7	37.951*
	July, 1969	6	53.122*
	August, 1969	6	7.217
	June, 1970	8	20.787*
	July, 1970	8	23.568*
	August, 1970	6	18.638*
	September, 1970	7	24.685*

* = $P < 0.05$

Table D-4. Results of the Wilcoxon rank sum test used to test for significant differences in the degree of stomach fulness between diurnal netting experiments.

Test comparison	Z	P
June 8-9 - June 22, 1969	2.091	0.0449*
June 8-9 - July, 1969	1.758	0.8480
June 8-9 - August, 1969	2.467	0.0189*
July - June 22, 1969	4.429	0.0001*
August - June 22, 1969	1.010	0.2396
August - July, 1969	1.394	0.1518
June - July, 1970	0.320	0.3790
June - August, 1970	2.596	0.0136*
June - September, 1970	0.744	0.2966
August - July, 1970	2.105	0.0431*
September - July, 1970	3.599	0.0006*
August - September, 1970	3.745	0.0003*

* = $P < 0.05$

Table D-5. Results of chi-square analyses between months for the occurrence of empty stomachs in adult and juvenile perch.

Test comparison	No. of fish		No. of empty stomachs		χ^2
June 8-8 - June 22, 1969	40	87	8	25	0.680
June 8-9 - July, 1969	40	71	8	28	3.568
June 8-9 - August, 1969	40	51	8	24	6.061*
June 22 - July, 1969	87	71	25	28	1.557
June 22 - August, 1969	87	51	25	24	3.948*
July - August, 1969	71	51	28	24	0.428
June - July, 1970	97	123	16	33	2.775
June - August, 1970	97	66	16	18	10.004*
June - September, 1970	97	86	16	9	0.940
July - August, 1970	123	66	33	18	0.011
July - September, 1970	123	86	33	9	7.542*
August - September, 1970	66	86	18	9	6.117*

* = $P < 0.05$

Table D-6. Results of chi-square analyses between locations and depths for the occurrence of major food items in juvenile perch stomachs.

Food item	Between locations July, 1970	Between locations Sept., 1970	Between depths
Daphnia	-	0.016	-
Gammarus	0.001	0.002	0.951
Hyalella	0.138	0.152	0.567
Crayfish	0.229	0.152	-
Fish	0.914	-	0.215
Diptera	0.170	-	0.175
Other insects	0.207	0.008	0.046

Table D-7. Results from Pearson's correlation analysis for seasonal changes of stomach fulness (A) and percent empty stomachs (B) with temperature (C) and average daylength (D).

Year	Test comparison	r
1970	A C	-0.7176
	A D	-0.7614
	B C	0.8867
	B D	0.3833
1969	A C	0.0741
	A D	-0.3470
	B C	0.9824*
	B D	0.9871*

* = $P < 0.05$

Table D-8. Summary of In stomach content weight ($X\ 10^3$) - In fork length linear regression analysis for all perch from 1969 and 1970.

b	s_b	CI ($P_{\pm} = 0.95$)	$s_{y.x}$	a	Analysis of Variance				
					Source	df	SS	MS	F
2.3659	0.2616	0.5651	0.4411	-6.0897	Total	14	18.437		
					Regression	1	15.908	15.908	81.79*
					Residual	13	2.529	0.195	

* = $P < 0.05$

Table D-9. Result of the t-test used to test b = 3.00 from the relationship between stomach content weight and fish length.

Calculated b	Theoretical b	Mean Square Dev. From Regression (s_b)	df	t
2.366	3.000	0.2616	13	2.424*

* = $P < 0.05$

Table D-10. Summary of ln stomach content weight per unit fish weight — time linear regression analyses carried out on juvenile perch digestion rate experiments.

Experiment Dominant Food	Temp. (C)	b	s_b	CI(P = 0.95) $\pm$	$s_{y.x}$	a	Analysis of Variance Source	df	SS	MS	F
June Daphnia	15	-0.1419	0.0047	0.0097	0.1296	5.4454	Total	13	11.537		
							Regression	1	11.335	11.335	674.70*
							Residual	12	0.202	0.017	
July Amphi-pods	20	-0.1220	0.0148	0.0563	0.2788	5.0035	Total	7	5.658		
							Regression	1	5.191	5.191	66.81*
							Residual	6	0.467	0.078	
Sept. Daphnia	13	-0.638	0.0024	0.0058	0.0583	5.3500	Total	8	2.454		
							Regression	1	2.430	2.430	714.8*
							Residual	7	0.024	0.033	

* = $P < 0.05$

Table D-11. Summary of covariance analyses between slopes of ln stomach content weight per unit fish weight ($\times 10^4$) -- time linear regression lines for juvenile perch digestion rate experiments.

Test comparison	slope	Deviations from regression df	SS	MS	F
July	-0.1220	6	0.4667	0.0777	
June	-0.1419	12	0.2018	0.0168	
		18	0.6685	0.0370	
Pooled	-0.1343	19	0.7480	0.0394	
Difference		1	0.0795	0.0795	2.149
June	-0.1419	12	0.2018	0.0168	
September	-0.0638	7	0.0242	0.0034	
		19	0.2260	0.0119	
Pooled	-0.1017	20	1.9900	0.9950	
Difference		1	1.7640	1.7640	148.240*
July	-0.1220	6	0.4665	0.0777	
September	-0.0638	7	0.0242	0.0034	
		13	0.4907	0.0378	
Pooled	-0.0853	14	1.2210	0.0872	
Differences		1	0.7303	0.7303	19.320*

* = $P < 0.05$